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ESTIMATES OF HARVEST POTENTIAL AND DISTRIBUTION OF THE DEEP SEA RED CRAB, *CHACEON QUINQUEDENS*, IN THE NORTHCENTRAL GULF OF MEXICO

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ABSTRACT Harvest potential, relative abundance, and geographic and bathymetric distribution are discussed for the red crab, *Chaceon quinquedens*, in the northcentral Gulf of Mexico. Harvest potential is expressed as the number of trapable crabs present on fishing grounds defined as depths ranging from 677 m to 1043 m between 87.5° and 88.5°W longitude. Using various estimates of the effective fishing area (EFA) of a trap, the number of trapable red crabs on the fishing grounds ranged from 3.7×10^6 to 10.7×10^6. Estimates of crab numbers suggest there is a potential for commercial harvest in the northcentral Gulf of Mexico, east of the Mississippi River. However, fishery development must take into consideration the preponderance of females on the defined fishing grounds (M:F ratio = 1:2.1) and the high incidence of ovigerous females (~20%) during much of the year. Females generally dominated at all depth strata, but the proportion of males to females increased with depth. Reduced numbers of red crabs were collected off the western Louisiana coast and a shift in depth distribution was found. Minimum upper depth limit for red crabs west of the Mississippi River was 860 m as compared to 677 m east of the River. The known range of *C. fenneri* is extended to 92°12"W longitude.

INTRODUCTION

Deep-water crabs of the family Geryonidae are distributed worldwide. Manning and Holthuis (1989) revised the family to include two new genera and nine new species. The majority of geryonid species were placed in the genus *Chaceon*. The genus *Geryon* was restricted to two species, *G. longipes* and *G. trispinosus*, both from the northeastern Atlantic Ocean. Deep-water fisheries for geryonid crabs are conducted along both sides of the Atlantic Ocean. Eastern Atlantic fisheries for *C. maritae* exist off Namibia in southwest Africa (Melville-Smith 1988), and commercially exploitable quantities of *C. maritae* are found off the Ivory Coast, Congo, and Angola (Beyers and Wilke 1980). In the western Atlantic, a fishery for *C. quinquedens* was initiated in the northeastern United States in 1973 and 1974 (Ganz and Herrmann 1975). In 1980, the catch from this fishery was 2500 metric tons (Lux et al. 1982). Other western Atlantic species of *Chaceon* supporting limited commercial fisheries include *C. inghami* off Bermuda (Luckhurst 1986; Manning and Holthuis 1986) and *C. fenneri* off Fort Lauderdale, Florida (Erdman and Blake 1988).

Faunal surveys conducted by the National Marine Fisheries Service (Mississippi Laboratories) and Pequegnat (1970) suggest that geryonid crabs are widely distributed throughout the Gulf of Mexico. Lockhart et al. (1990) identified seasonal, geographic, and bathymetric distribution of *C. fenneri* and *C. quinquedens* in the eastern Gulf of Mexico. Red crabs occurred across the geographic arc sampled, with overall population densities and relative proportion of females highest in the northcentral Gulf of Mexico. Distribution of red crabs in this study was not explained by bottom type, temperature, or interspecific competition, and it was suggested that observed distributional patterns of *Chaceon* in the eastern Gulf of Mexico may be tied to reproductive strategies. Based on the timing of larval release (Erdman and Blake 1988; Erdman et al. 1991; Perry et al. 1991) and the concentration of females in the northward portion of the study range, a causal role for the Loop Current in red crab population structure was proposed.

There has been considerable interest in fishing for deep sea crabs in the Gulf of Mexico. However, efforts at fishery development have been hampered by lack of information on areal and bathymetric distribution patterns and estimates of stock abundance. The present study addresses the distribution, abundance, and harvest potential of *C. quinquedens* in the northcentral Gulf of Mexico.

MATERIALS AND METHODS

This study was designed to establish the geographic and bathymetric limits of *Chaceon* species and to determine their relative abundance from 88° to 93°W longitude. Cruises were made in May and August 1989 onboard the Gulf Coast Research Laboratory's 29.7 m steel-hulled research vessel, the R/V *Tommy Munro*. Five areas (1, 6-9) were selected for sampling (Figure 1, Table 1). Area 1 was also sampled by Lockhart et al. (1990). Trap lines were deployed at three selected depths on the day of arrival in an area and were retrieved the following day. Sample depth was varied between the spring and summer cruises to cover bathymetric distributions of *C. fenneri* and *C. quinquedens* as reported by Pequegnat (1970) and Lockhart et al. (1990). Depths sampled in May were 494, 677, and 860 m in all areas. In August, traps were set at 311, 860, and 1043 m in all areas, with the exception of Area 1 where traps were set at 860, 1043, and 1830 m. The single set at 1830 m in Area 1 was an exploratory set to examine the lower depth limit of red crabs and was not used in statistical analyses of catch data.

Sampling protocol was similar to that followed by Lockhart et al. (1990) with the exception that limited deck space necessitated use of the smaller, stackable Fathoms-Plus® trap in addition to the Nielsen designed trap (Erdman and Blake 1988). Seven Fathoms-Plus® plastic traps and a single Nielsen trap were fished at each depth within an area. Traps were baited with mixed fish (*Peprilus burti*, Gulf butterfish; *Micropogonias undulatus*, Atlantic croaker; *Brevoortia patronus*, Gulf menhaden). Trap lines were set

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and retrieved using a hydraulic net reel with a 1.2 m by 1.5 m spool and stern-mounted hydraulic A-frame. Traps were attached to a groundline of 1.6 cm polypropylene, 732 m in length. Beckets were spliced at intervals of 92 m for attachment of traps fished on 2 m gangions. Anchors (23 kg) were attached at both ends of the groundline. A buoyline of 1.3 cm polydacron/nylon was deployed at one end of the trap line at a scope of 2.5 times the depth. Traps were set with the vessel under power during deployment of both groundline and buoyline to ensure proper spacing between traps along the predetermined depth contour. Fishing duration ranged from 18 to 22 hours.

On retrieval of the trap line, contents of each trap were separated into species and the crabs were placed in numbered baskets in chilled seawater. Sex and carapace width (mm) were determined for all individuals. Females were examined for presence of eggs or egg remnants, and egg mass color was noted. Bottom water temperatures were measured at each trap site with a reversing thermometer.

The effective fishing area per trap (EFA) was calculated using the method of Miller (1975) which assumed that each trap fished a circular area with a radius of one half the distance between adjacent traps. In calculations of EFA of a trap, it is assumed that all traps fish the same, i.e. that there are no significant differences (alpha = 0.05) among the catch/trap along the trap line. To test this hypothesis, the catch/trap of all traps was statistically analyzed using one-way ANOVA and a multiple range test (Duncan's method). An estimate of the number of trapable crabs on the fishing grounds of the northcentral Gulf of Mexico was calculated using the formula provided by McElman and Elner (1982):

$$\# \text{trapable crabs} = \frac{1}{\text{EFA (km}^2/\text{trap)}} \times \frac{\text{mean \# crabs}}{\text{trap}} \times \text{fishing grounds (km}^2)$$
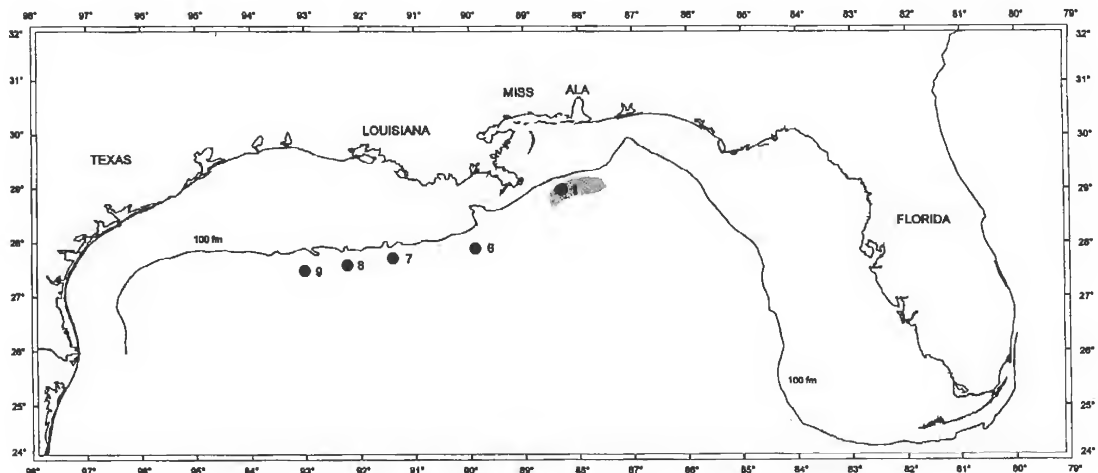

Figure 1. Location of sampling areas and fishing grounds (shaded area).

TABLE 1

Station locations by area, depth, latitude and longitude.

Area	Depth (m)	Latitude (°N)	Longitude (°W)
1	494	88°23.00	29°03.73
1	677	88°24.64	29°00.59
1	860	88°19.27	28°59.67
1	1043	88°19.23	28°56.02
1	1830	88°08.59	28°44.08
6	311	90°00.01	28°06.50
6	494	89°56.83	27°58.50
6	677	89°55.88	27°56.25
6	860	89°54.74	27°53.86
6	1043	89°51.39	27°47.95
7	311	91°22.71	27°50.59
7	494	91°18.38	27°47.82
7	677	91°21.18	27°44.71
7	860	91°23.84	27°43.20
7	1043	91°25.80	27°36.56
8	311	92°04.52	27°47.78
8	494	92°11.89	27°39.98
8	677	92°12.39	27°37.65
8	860	92°13.99	27°35.44
8	1043	92°08.77	27°33.39
9	311	93°02.21	27°39.15
9	494	93°07.77	27°33.29
9	677	93°03.00	27°32.88
9	860	93°00.11	27°29.16
9	1043	93°08.12	27°22.58

Fishing grounds were defined using red crab distribution and abundance data from Lockhart et al. (1990) and the present study. Fishing grounds were located at depths from 677 to 1043 m between 87.5° and 88.5°W longitude and encompassed approximately 1200 km².

Male to female abundance by trap set, catch/trap by depth, and catch/trap by season were statistically analyzed by a paired comparison of difference in abundance. Results are reported using a t-statistic with alpha set at 0.05. Carapace width of males and females was compared using a two sample analysis of means assuming unequal variances (t-test, alpha = 0.05). Percent of catch of commercial size was determined for males and females by area.

RESULTS

Temperature

Bottom water temperatures within depth strata ranged from 11.4 to 12.7°C at 311 m, 8.0 to 8.8°C at 494 m, 6.4 to 7.2°C at 677 m, 5.6 to 6.0°C at 860 m, and 5.2 to 5.6°C at 1043 m. Temperature was not taken at the deepest depth sampled, 1830 m. Bottom water temperatures decreased with depth, and the range in temperature within a depth stratum narrowed with increasing depth. In May, for stations west of the Mississippi River, temperatures tended to increase from east to west within the 494 and 677 depth strata. Comparative seasonal data are available only for the

860 m sampling depth, and there was little difference in the temperature extremes between May (5.6 to 6.0°C) and August (5.8 to 6.0°C).

Distribution Studies

Carapace width (CW), sex, male to female ratio, and bathymetric distributions by area and season were recorded for *C. quinquedens* (Table 2). Mean carapace width per trap set ranged from 109 to 140 mm for females and 95 to 143 mm for males. Smallest crabs occurred in deeper depths west of the Mississippi River in Areas 8 and 9. Overall mean carapace width of males (128 mm) was significantly different from the mean carapace width of females (116 mm), (P = 0.00, t = 1.97 at 458 df). Total number of male and female crabs and total number of crabs $\geq$ 114 mm CW (minimum size for harvest in the Atlantic fishery as reported by Armstrong 1990) were determined (Figure 2). In Area 1, east of the Mississippi River, 99% of males and 61% of females were $\geq$ 114 mm CW. Combining all areas, 87% of the males and 63% of females were of commercial size, with 81% of all crabs $\geq$ 114 mm CW regardless of sex. Areas 1 and 9 produced 65% and 17% of the red crabs taken, respectively (Figure 3). Contribution to total catch was between 3% and 7% for all other areas (6-8).

Average catch/trap set by sex at all areas, depths, and seasons in sets where crabs were caught was used to compare abundance of males versus females. There was a significant difference in the mean number of males to females per trap set (P = 0.02, t = 2.57 at 17 df). Mean number of males per trap set was 18.2, compared to 38.6 for females. The ratio of males to females varied from 0:1.0 to 1.0:32 among trap sets (Table 2), with females twice as abundant as males overall (M:F = 1.0:2.1).

Bathymetric distribution as a function of mean catch/trap by area and season is shown in Tables 3 and 4. The highest overall mean catch/trap was 23.8 crabs at 677 m in May at Area 1. With the exception of the shallowest depth (494 m, n = 1), mean catch/trap in Area 1 was not significantly different between sampled depth strata for May ($\bar{x}$ = 23.8 at 677 m and $\bar{x}$ = 16.9 at 860 m) or August ($\bar{x}$ = 20.9 at 860 m and $\bar{x}$ = 19.3 at 1043 m). Catch/trap for Area 6 was not statistically compared between seasons due to lost trap lines. Mean catch/trap for Areas 7, 8, and 9 was compared between 860 m and 1043 m depths for August. In Area 7, there was no significant difference in mean catch/trap at 860 m ($\bar{x}$ = 2.8) and 1043 m ($\bar{x}$ = 2.6). For Area 8, mean catch/trap was significantly greater at 1043 m ($\bar{x}$ = 6.6)

than at 860 m ($\bar{x}$ = 1.6; P = 0.00, t = 4.61 at 7 df). The reverse was true for Area 9; there was a significantly higher catch/trap at 860 m than at 1043 m (P = 0.01, t = 3.90 at 7 df). Mean catch/trap at 860 m was 9.6, compared to 3.9 crabs at 1043 m. Catch/trap was used to compare seasonality of catch at the common depth of 860 m at each area. No significant differences in mean catch/trap were found at any area between May and August at 860 m.

Upper depth limit of red crabs west of the Mississippi River (Areas 6-9) was 860 m, compared to 677 m for crabs taken in Area 1, east of the River. Catches of a single crab at 494 m in Area 1 and at 677 m in Area 7 were considered solitary events and were not used in defining the observed upper depth limit.

Recent oviposition in *C. quinquedens* is indicated by the presence of orange egg masses; eggs become purple-black prior to hatching (Haefner 1977). Seventeen percent of all females collected in May were ovigerous, with either orange or brown egg masses. Egg remnants were recorded on the pleopods of 11 individuals. Ovigerous females collected in August comprised 18% of all females. Egg colors were predominantly brown, and no egg remnants were observed. Ovigerous females were more abundant at the shallower depths of their bathymetric distribution (677 and 860 m). The size range of ovigerous females in August (95-135 mm CW) was comparable to those collected during May (100-130 mm CW). One immature female crab (64 mm CW) was taken at 860 m in May in Area 6.

A comparison among catch/trap by trap number was performed with one-way ANOVA and a multiple range test (Duncan's method). These tests were applied over all areas, depths, and seasons in sets where crabs were caught. The mean catch of end traps (traps 1 and 8) was 7.0 and 9.6, respectively, compared to the mean catch of inner traps (traps 2 through 7, $\bar{x}$ range = 6.1 to 11.3). The Nielsen trap had the highest mean catch/trap ($\bar{x}$ = 11.3) due to two high catches in Area 1. Statistically significant differences in mean catch were not found among crab traps (ANOVA). Catch was found to be homogeneous among traps (multiple range test). The EFA/trap was calculated to be 6,647 m². Based on the formulas of McElman and Elner (1982) and Miller (1975), the estimated number of trapable red crabs was extrapolated to be 3.7 x 10⁶ on a calculated fishing ground of 1,200 km².

Chaceon fenneri was not abundant in the study area. Golden crabs occurred in samples in May. Four specimens were taken in Area 6 (3 at 494 m, 1 at 677 m). Areas 7 and 8 each produced a single crab at 494 m.

TABLE 2

Summary of catch data of *Chaceon quinquedens* in the northcentral Gulf of Mexico.

| Date | Area | Depth Meters | Males | | | | Females | | | | Total No. | Ratio M/F |
| | | | Carapace Width | | | | Carapace Width | | | | | |
			Mean	Max.	Min.	No.	Mean	Max.	Min.	No.		
05/15/89	1	494				0	130	130	130	1	1	0:1
05/15/89	1	677	133	147	122	42	116	144	93	148	190	1:3.5
05/15/89	1	860	132	145	108	45	114	133	95	90	135	1:2
05/13/89	6	494				0				0	0	
05/13/89	6	677				0				0	0	
05/13/89	6	860	143	143	143	1	120	140	64	10	11	1:10
05/13/89	7	494				0				0	0	
05/11/89	7	677				0	140	140	140	1	1	0:1
05/11/89	7	860	140	140	140	1	128	139	110	28	29	1:28
05/09/89	8	494				0				0	0	
05/09/89	8	677				0				0	0	
05/09/89	8	860				0	118	125	112	6	6	0:6
05/07/89	9	494				0				0	0	
05/07/89	9	677				0				0	0	
05/07/89	9	860	130	136	125	2	114	135	98	64	66	1:32
08/12/89	1	860	134	148	123	61	115	137	95	106	167	1:1.7
08/12/89	1	1043	132	147	118	98	114	132	94	56	154	1.8:1
08/14/89	1	1830	127	133	123	3	114	123	103	16	19	1:5.3
08/10/89	6	311*										
08/10/89	6	860*										
08/10/89	6	1043	129	140	120	8	118	132	102	18	26	1:2.3
08/08/89	7	311				0				0		
08/08/89	7	860	138	141	136	5	129	142	114	17	22	1:3.4
08/08/89	7	1043	139	151	127	2	126	137	117	19	21	1:9.5
08/06/89	8	311				0				0		
08/06/89	8	860	135	140	130	2	130	142	109	11	13	1:5.5
08/06/89	8	1043	95	137	63	40	109	131	76	13	53	3.1:1
08/04/89	9	311				0				0		
08/04/89	9	860	125	144	89	9	111	127	92	68	77	1:7.6
08/04/89	9	1043	120	139	95	8	110	131	85	23	31	1:2.9

* Trap line lost
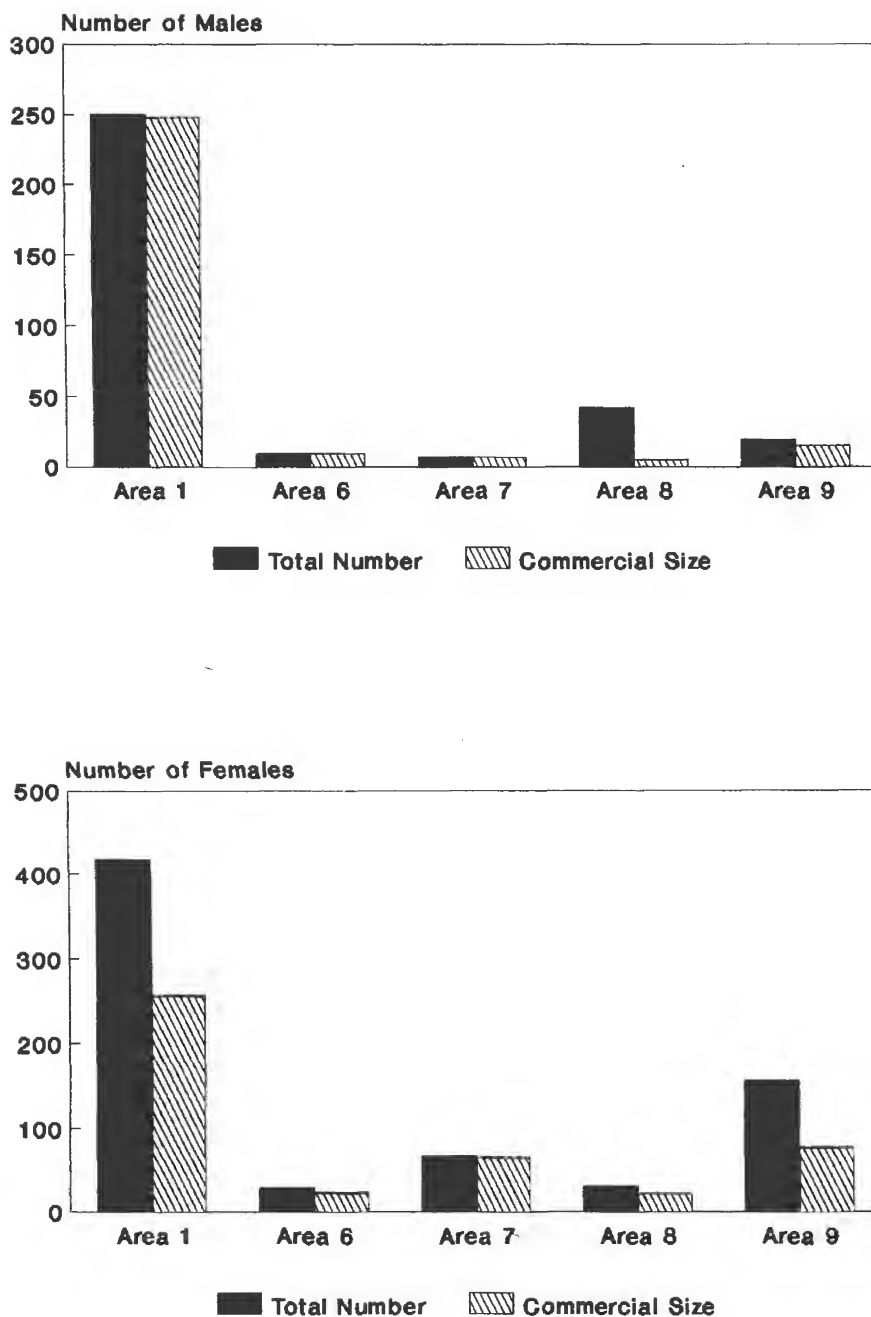
Figure 2. Total number of male and female *Chaceon quinquedens* ≥ 114 mm carapace width.
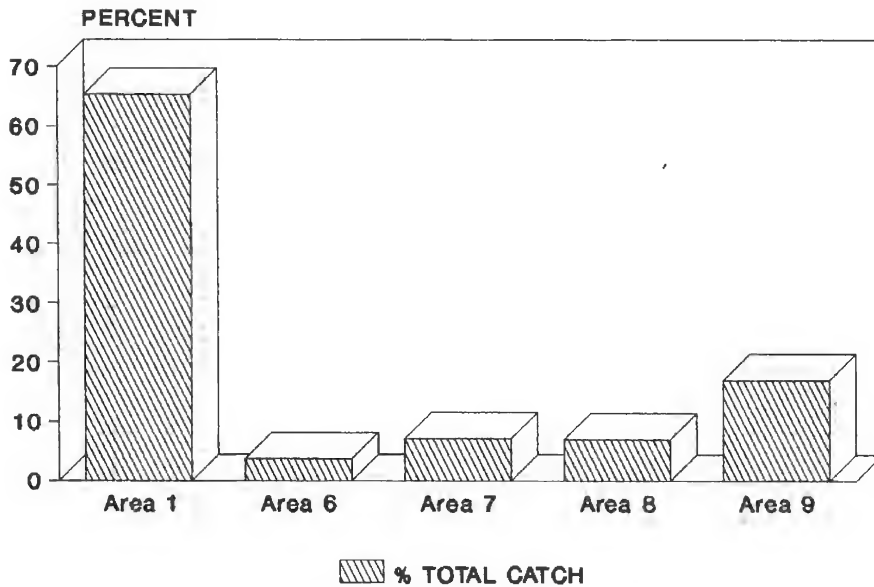
PERCENT

Figure 3. Percent catch, *Chaceon quinquedens*, by area.

DISCUSSION

Bathymetric and Geographic Distribution

Previous reports of geryonid crabs in the Gulf of Mexico include references to two species. Data from trawl surveys contain records of *C. quinquedens* and *C. affinis* (NMFS, Mississippi Laboratories). Pequegnat (1970) recorded *C. quinquedens* in the northern Gulf of Mexico and in the Caribbean. With the recognition and description of *C. fenneri* from slope waters of the western Atlantic and Gulf of Mexico, it is probable that early accounts of *C. affinis* from the eastern Gulf of Mexico are referable to *C. fenneri* (Manning and Holthuis 1984). Otwell et al. (1984) found *C. fenneri* common in the Gulf of Mexico at depths ranging from 384 to 641 m within latitudes 29°03' and 26°50' and longitudes 84°50' and 85°32'.

Lockhart et al. (1990) described the distribution of red and golden crabs in the eastern Gulf of Mexico and noted that there were geographic and bathymetric differences in distribution and abundance. They found red crabs widely distributed in the eastern Gulf of Mexico at depths of 677 m, their deepest sampling depth and the upper limit of red crab distribution. Highest concentrations were found in the

northcentral Gulf of Mexico between 87.5 and 88.5°W longitude. A supplemental sample taken during their study found red crabs at 900 m in that area. Golden crabs were more restricted in geographic distribution, with abundance centered in slope waters below 28°N latitude. They occurred at all depths sampled, but were most abundant at the shallower depths (311 and 494 m). Golden crabs were not abundant in our study (n = 6); thus geographic and bathymetric data are limited. Based on our samples, the known range of *C. fenneri* is extended to the western Gulf of Mexico (92°12"W longitude).

Bathymetric distribution of red crabs differed east and west of the Mississippi River. Red crabs were taken consistently at the 677 m sampling depth in the eastern Gulf of Mexico. However, the upper depth limit for red crabs west of the Mississippi River was 860 m. Although there was a downward shift in bathymetric distribution west of the River and different depth strata were sampled in May and August, a differential distribution by sex and depth was observed. While females outnumbered males at most depths sampled (two exceptions), the proportion of males to females increased at deeper depths. Approximately the same number of individuals were taken at the 860 and 1043 m sampling depths west of the River, indicating that deeper

TABLE 3
Catch per trap by area and depth for May 1989.

	Area 1			Area 6				Area 7			Area 8			Area 9		
	494 m	677 m	860 m	494 m	677 m	860 m	1,043 m	494 m	677 m	860 m	494 m	677 m	860 m	494 m	677 m	860 m
Trap #1	1	16	13	*	0	0	2	0	0	8	0	0	0	0	0	10
Trap #2	0	26	17		0	0	0	0	1	1	0	0	1	0	0	6
Trap #3	0	10	9		0	0	1	0	0	4	0	0	3	0	0	10
Trap #4	0	20	8		0	0	1	0	0	1	0	0	2	0	0	4
Trap #5	0	30	30		0	0	4	0	0	6	0	0	0	0	0	2
Trap #6	0	34	13		0	0	1	0	0	3	0	0	0	0	0	8
Trap #7	0	17	20		0	0	1	0	0	2	0	0	0	0	0	9
Trap #8	0	37	25		0	0	1	0	0	4	0	0	0	0	0	17
Total	1	190	135		0	0	11	0	0	29	0	0	6	0	0	66
Mean	0.125	23.750	16.875		0.000	0.000	1.375	0.000	0.125	3.625	0.000	0.000	0.750	0.000	0.000	8.250
Std. Dev.	0.331	8.899	7.236		0.000	0.000	1.111	0.000	0.331	2.288	0.000	0.000	1.090	0.000	0.000	4.265
Variance	0.109	79.188	52.359		0.000	0.000	1.234	0.000	0.109	5.234	0.000	0.000	1.188	0.000	0.000	18.188

TABLE 4
Catch per trap by area and depth for August 1989.

	Area 1			Area 6			Area 7			Area 8			Area 9		
	860 m	1,043 m	1,830 m	311 m	860 m	1,043 m	311 m	860 m	1,043 m	311 m	860 m	1,043 m	311 m	860 m	1,043 m
Trap #1	15	19		*	*	9	0	4	2	0	3	3	0	8	6
Trap #2	17	13				1	0	2	0	0	1	5	0	5	7
Trap #3	20	9				7	0	1	1	0	1	6	0	4	0
Trap #4	15	14				6	0	5	5	0	0	10	0	11	4
Trap #5	49	44				3	0	1	1	0	0	3	0	13	6
Trap #6	19	11				0	0	3	2	0	2	8	0	13	3
Trap #7	19	26				0	0	6	2	0	6	6	0	11	1
Trap #8	13	18				0	0	6	8	0	6	12	0	12	4
Total	167	154	19			26	0	22	21	0	13	53	0	77	31
Mean	20.875	19.250				3.250	0.000	2.750	2.625	0.000	1.625	6.625	0.000	9.625	3.875
Std. Dev.	10.868	10.604				3.382	0.000	1.984	2.446	0.000	1.932	2.997	0.000	3.314	2.315
Variance	118.109	112.438				11.438	0.000	3.938	5.984	0.000	3.734	8.984	0.000	10.984	5.359

* Trap line lost

sampling depths were well within the bathymetric range of this species.

Lockhart et al. (1990) discussed the distribution of red crabs in the eastern Gulf of Mexico in relation to bottom sediment type and temperature. They concluded that neither temperature nor bottom type fully explained red crab distribution. Similar sediment types (silt, clayey silt, silty clay, clay) are found across the northcentral Gulf of Mexico (Uchupi and Emery 1968; Gallaway et al. 1988); thus reduced catches of red crabs west of the Mississippi River and the absence of red crabs at shallower depths in the present study do not appear to be explained by bottom type. Because bottom water temperatures at sampling depths within and among areas were not appreciably different, temperature does not seem to be the controlling factor in depth distribution. Working off New England, Haefner (1978) reported taking red crabs at depths as shallow as 200 m in temperatures as high as 12°C, further compounding the disparate depth distribution and temperature data for this species.

Data from Area 1 corroborated the observations of Lockhart et al. (1990) on the population structure of *C. quinquedens* in the eastern Gulf of Mexico. Females were preponderant in our samples in this area and outnumbered males 2.1:1. Although Lockhart et al. (1990) sampled only at the upper depth limit of red crab distribution in the eastern Gulf of Mexico, they noted that the abundance of females in the northern Gulf of Mexico coupled with the lack of females to the south may indicate migration of females northward. Melville-Smith (1987 a,b,c) reported that *C. maritae* females exhibited significant directional movement and that this movement was counter to the prevailing surface currents. The concentration of females northward of their sampled range, their occurrence in shallower, warmer waters, and the timing of larval release led Lockhart et al. (1990) to suggest that distribution of *Chaceon* in the eastern Gulf of Mexico may be tied to reproductive strategy; specifically, larval transport and recruitment. They proposed a causal role for the Loop Current System in basic life history adaptations and suggested that larvae released in February and March, a time of minimal penetration of the Loop Current, would avoid entrainment and flushing from the system. While this assumption may hold true during some years, the extent of northward incursion of the Loop Current into the Gulf of Mexico is highly variable, and maximum intrusion can occur during any season (Vukovich et al. 1978). Cooper and Humphreys (1981) noted that "it is difficult if not impossible to identify a typical Loop Current position with any given season or month." Circulation processes in the Gulf of Mexico are complex and variable, and while

observed distribution may be tied to reproductive strategies, the relationship of biological processes to physical mechanisms remains speculative.

Commercial Potential

Area 1 produced 65% of the red crabs taken during this study and is the only area sampled that showed potential for fishery development. Mean catch/trap in Area 1 was similar at each depth stratum for May and August, with highest overall mean catch/trap (23.8) occurring at 677 m in May (Tables 3 and 4). Catch/trap rates in this area compare favorably with those reported in the New England red crab fishery (Ganz and Herrmann 1975), particularly in light of the high percentage (81%) of market size crabs (≥ 114 mm CW) taken in this study. These rates are also comparable to the highest rates reported by Wenner et al. (1987) for golden crabs in the South Atlantic Bight off South Carolina.

Estimates of red crab population densities derived from trap studies were made by Stone and Bailey (1980) and McElman and Elner (1982) along the Scotian Shelf. Using a study area of 2767 km², Stone and Bailey (1980) projected population densities of 2.3 x 10⁶. McElman and Elner (1982) provided various population estimates for their study area based on changing EFAs. Lowest estimates used an EFA of 4,100 m² to produce 2.8 x 10⁶ crabs. Highest population estimates were based on an EFA of 2300 m² which produced an estimate of 5 x 10⁶ crabs. Because greater catches at end traps did not occur in their studies, these authors suggested that there was no overlap in fishing area in traps placed 54 m (Stone and Bailey 1980) and 62 m apart (McElman and Elner 1982). They noted that density and biomass estimates were best based on an EFA of 2300 m². Using an EFA of 6647 m², we calculated minimum crab densities of 3.7 x 10⁶ on the northcentral Gulf of Mexico fishing grounds. If we assume an EFA of 2300 m² for the total calculated fishing grounds (1200 km²), our estimate of population size would increase to 10.7 x 10⁶ crabs. An intermediate EFA of 3000 m² would produce a population estimate of 8.1 x 10⁶ crabs. Based on these catch rates, the red crab in our calculated area could potentially support a small commercial fishery. Fishery development, however, must take into consideration the preponderance of females on the fishing grounds (M:F ratio 1:2.1) and the incidence of ovigerous females (~20%) during much of the year (Lockhart et al. 1990 and present study). In addition, data on recruitment to fishing grounds as well as information on critical life history parameters are necessary before fishery development is encouraged.

ACKNOWLEDGMENTS

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Observations on Extant Populations of the Softshell Clam, *Mya arenaria* Linné, 1758 (Bivalvia: Myidae), from Georgia (USA) Estuarine Habitats

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OBSERVATIONS ON EXTANT POPULATIONS OF THE SOFTSHELL CLAM, *MYA ARENARIA* LINNÉ, 1758 (BIVALVIA: MYIDAE), FROM GEORGIA (USA) ESTUARINE HABITATS

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ABSTRACT The softshell clam, *Mya arenaria* Linné, 1758, is reported from Georgia (USA) estuarine habitats based on studies conducted between 1969 and 1972. Observations on Georgia estuarine habitats where extant populations of softshell clams occurred are described. On several occasions, fresh shells with periostracum and tissue remnants were found in a brackish drainage system on Sapelo Island. These shells represent the first southern records of extant populations of softshell clams from such a specialized habitat type. Living specimens of *M. arenaria* from the benthos and specimens in the stomach contents of stingrays (*Dasyatis sabina*) were collected at four stations during 1969 in the North and South Newport Rivers, mesohaline tidal systems forming part of the southern and northern headwaters of St. Catherines and Sapelo Sounds. The stomach of a stingray collected near the mouth of Little Ogeechee River during another study also contained specimens of *M. arenaria*. Ephemeral, intertidal, winter populations of juvenile softshell clams are reported from exposed pleistocene beach faces along tidal rivers in Chatham, Georgia. The associated fauna collected with softshell clams and occurrence of other cold temperate and boreal species from Georgia estuaries are discussed. The distribution of *M. arenaria* appears to be mainly limited by a critical maximum temperature of 28°C. The relatively cooler summer temperatures observed at the Sapelo Island tidal ditch site may enable the species to survive in this restricted habitat. Data from the present study indicate that during winter and spring, softshell clams appear to be bionomically important components of the benthos and the diet of stingrays in some Georgia estuarine habitats. Whether or not reproducing populations of *M. arenaria* occur year-round in Georgia estuaries still remains an open question.

INTRODUCTION

Between 1967 and 1972, we made a series of collections and observations on two estuarine habitats, one associated with tidally influenced brackish water ditches on Sapelo Island, the other in the subtidal upper reaches of St. Catherines and Sapelo Sounds. These two habitats have been generally described in earlier publications dealing with other faunal studies (Sikora et al. 1972; Heard 1975; Rasmussen 1994).

At some of the study sites in these two areas, we were able to document the presence of extant populations of the softshell clam, *Mya arenaria* Linné, 1758, a commercially important bivalve (Hanks 1963; Pileggi and Thompson 1979) commonly known to northern temperate and boreal coastal habitats of Europe and North America (Theroux and Wigley 1983).

HISTORICAL

Mya arenaria has existed along the North American and European coasts since the Pliocene, but died out in Europe during the Ice Age at the beginning of the Pleistocene

(Strauch 1972), after which it later became reestablished. Since the larvae could not have spread spontaneously to Europe from America, it was previously assumed that *M. arenaria* was reintroduced to Europe by man in the 16th century after the voyage of Columbus (Hessland 1946). Recent findings by Danish geologists, however, imply a reestablishment of the species in Europe much earlier, about 1200, probably by Viking voyagers. This is supported by carbon-dated analyses of shell material of *M. arenaria* from Holocene layers in the Kattegat region, Jutland (Petersen et al. 1992).

Extant populations of *Mya arenaria* are presently known or reported from most of western Europe, from the East Coast of the United States (Labrador to Charleston, South Carolina), from isolated populations in the Arctic, and from introduced populations established along the Pacific coast of North America (Foster 1946; La Rocque 1953; Ockelmann 1958; Tebble 1966; Laursen 1966; Abbott 1968, 1974; Emerson et al. 1976; Bernard 1979; Theroux and Wigley 1983; Abbott and Dance 1986). Because of its broad range in the northern hemisphere, various authors have placed the softshell clam in the following six zoogeographical faunal provinces: Virginian, Boreal, Celtic, Transatlantic, Aleutian Californian,

and Japonic (Coomans 1962; Gosner 1971; Dance 1974). None of these authors, however, mention the occurrence of *M. arenaria* in the Carolinian Province.

Records of softshell clams from the Carolinian Province are sparse and vague. According to Foster (1946), the North Carolina record (from Beaufort) is based on dead valves only. Abbott's (1968) South Carolina record is not documented or repeated in any of his later publications and may be an error. Regarding its North American, East Coast occurrence, Theroux and Wigley (1983: 48) state, "The normal distribution of the softshell clam is from Labrador to South Carolina, extending, locally, south to Florida.." The record from South Carolina is based on specimens from a population near Charleston; these specimens are housed in the Woods Hole Collections of the National Marine Fisheries Service. However, Theroux and Wigley (1983) cite no published or unpublished references to specimens or collection sites for the occurrence of softshell clams in Florida waters.

There are several nominal published records for *Mya arenaria* from Georgia estuarine waters. Two of these records are only mentioned in footnotes (Sikora et al. 1972:518; Howard et al. 1973:43). Howard and Frey (1975a) reproduced Heard and Heard's (1971) unpublished list of the common invertebrates of Sapelo and St. Catherines Sounds which included records of softshell clams from the mesohaline waters of the North Newport River system. Extant specimens of *M. arenaria* were listed from the Turtle River (St. Simmons Sound) and St. Marys River (Florida-Georgia border) by Howard and Frey (1975b) and from Doboy Sound by Mayou and Howard (1975). Frey et al. (1975:271) reported softshell clams from tidal river channels throughout the Georgia coast and considered this bivalve as one of several "best indicators of present-day estuarine environments in Georgia." Later, Howard et al. (1977:341) briefly mentioned the presence of *M. arenaria* in the diet of stingrays from Georgia estuaries.

MATERIALS AND METHODS

Sapelo Island Collection Sites

Sapelo Island is located off the coast of Georgia (Figure 1). The island study site was in a brackish-water drainage ditch under High Point Road (culvert then present). This ditch is part of the head waters of Barn Creek, which empties into the Duplin River, a northeastern arm of Doboy Sound, about 800 m NNW of the Sapelo Island air field (Figure 2). The

general ecological characteristics of the tidal ditch habitats in this area have been described earlier by Rasmussen (1994). The collection site is located in an isolated area surrounded and shaded by a dense, mixed hardwood-pine forest. The water level was influenced by regular tides from the Duplin River. On the landward side of the ditch, the often strong currents through the culvert had created a pool, approximately one meter deep, with a relatively firm bottom where the shell material of *Mya arenaria* was collected.

The site was visually inspected weekly from early June 1971 to early February 1972. Any changes were noted and any visible shells were collected by hand or with a dipnet. Water temperature was measured with a mercury thermometer and salinity was measured with a T/C refractometer (American Optical Corporation). Both measurements were taken just below the surface. An attempt was initially made to obtain sediment samples, but it was impossible to dig in the hard substratum.

North Newport River Collection Sites (Figure 3)

Specimens of *Mya arenaria* from this area were collected in 1969 during a baseline study to monitor possible ecological effects of a paper mill on Riceburro Creek, a headwater tributary of St. Catherines and Sapelo Sounds. Faunal and water-quality data (dissolved oxygen (DO), pH, salinity, temperature, turbidity) were gathered during 43 monthly cruises using the University of Georgia Marine Institute research vessel, *R/V Kit Jones*. The faunal collections were made monthly at 14 stations in Sapelo Sound, St. Catherines Sound and their adjacent tidal river tributaries (Figure 3). Four of these stations (10, 11, 12, and 13), all located in the head waters of Sapelo and St. Catherines Sounds (North and South Newport River systems), are relevant to this study. Stations 10, 11, 12, and 13 were sampled along a 300 to 400 m track in or immediately adjacent to the river channel in depths ranging from 4 to 8 m. Stations 10, 12, and 13 had a mostly sand-silt substratum. Station 11 had a mosaic of bottom types ranging from coarse gravel with fossil lag deposits (sharks teeth, whale bone, etc.) to mixed sand-silt and hard mud substrata. The channel margins along some or all parts of these station tracks were composed of consolidated pleistocene sand deposits.

Fish and large epibenthic invertebrates were collected with a 25-foot otter trawl, infaunal macroinvertebrates with a bucket dredge. Samples of the latter comprised all fauna retained by a 1 mm screen. A series of fish specimens from each station were kept for stomach-content analyses. Apart from a few voucher specimens and the fish for stomach-
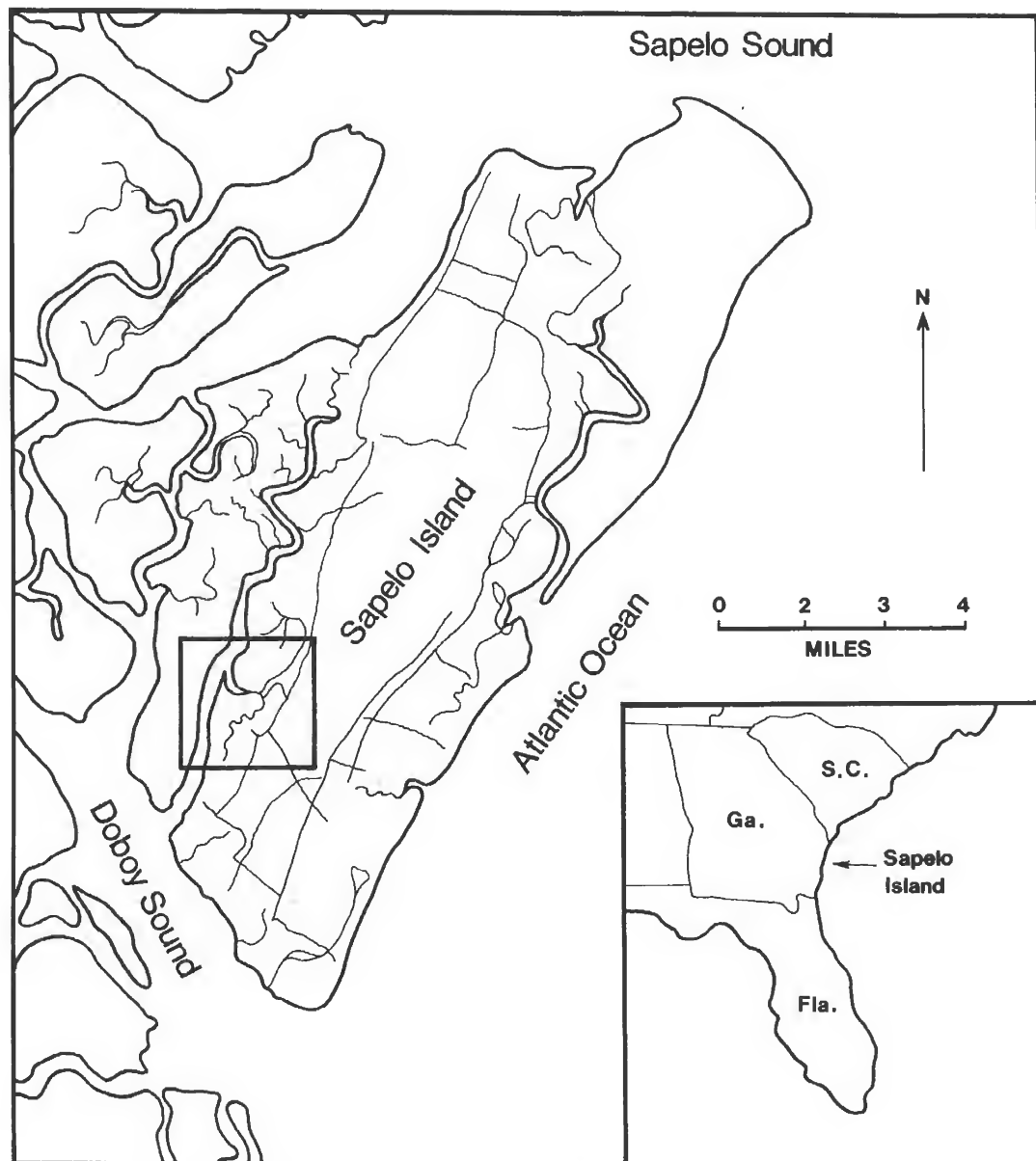
Figure 1. Map of Sapelo Island, Georgia, showing location on US East Coast (inset, lower right) and location of study area (framed, see Figure 2).
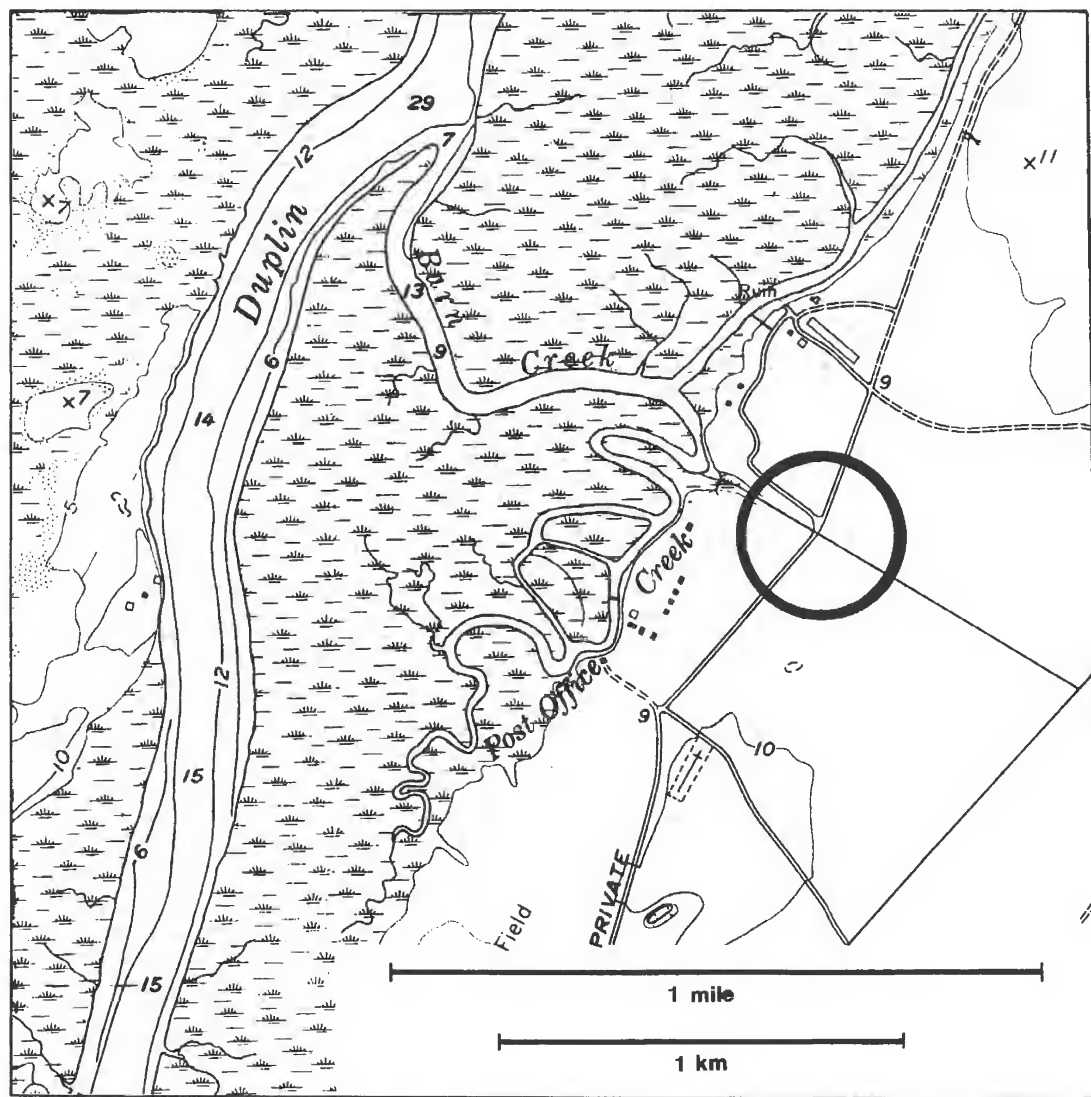
Figure 2. Enlarged map of study area on Sapelo Island, showing Duplin River, Barn Creek and Post Office Creek, leading to locality with *Mya arenaria* (circled). Depths in feet. Map from Doboy Sound, GA. N3122-W8115/7.5. US Department of Commerce Coast and Geodetic Survey, edited and published by the US Geological Survey, 1954.

content analyses, most fish and large macroinvertebrates were identified and counted while alive, then thrown overboard. All fish and sieve residues retained were fixed onboard in a 4% solution of formaldehyde in seawater, later washed in freshwater and transferred to 70% ethanol. Further analyses and taxonomic studies were done in the laboratory.

Representative specimens of *Mya arenaria* collected during this study with the bucket dredge are deposited in the National Museum of Natural History (USNM), the Zoological Museum, University of Copenhagen (ZMUC), and the Gulf Coast Research Laboratory Museum (GCRL). Common names for the mollusks, decapod crustaceans, and fishes used in this paper are from American Fisheries Society Special Publications 6, 16, and 17.
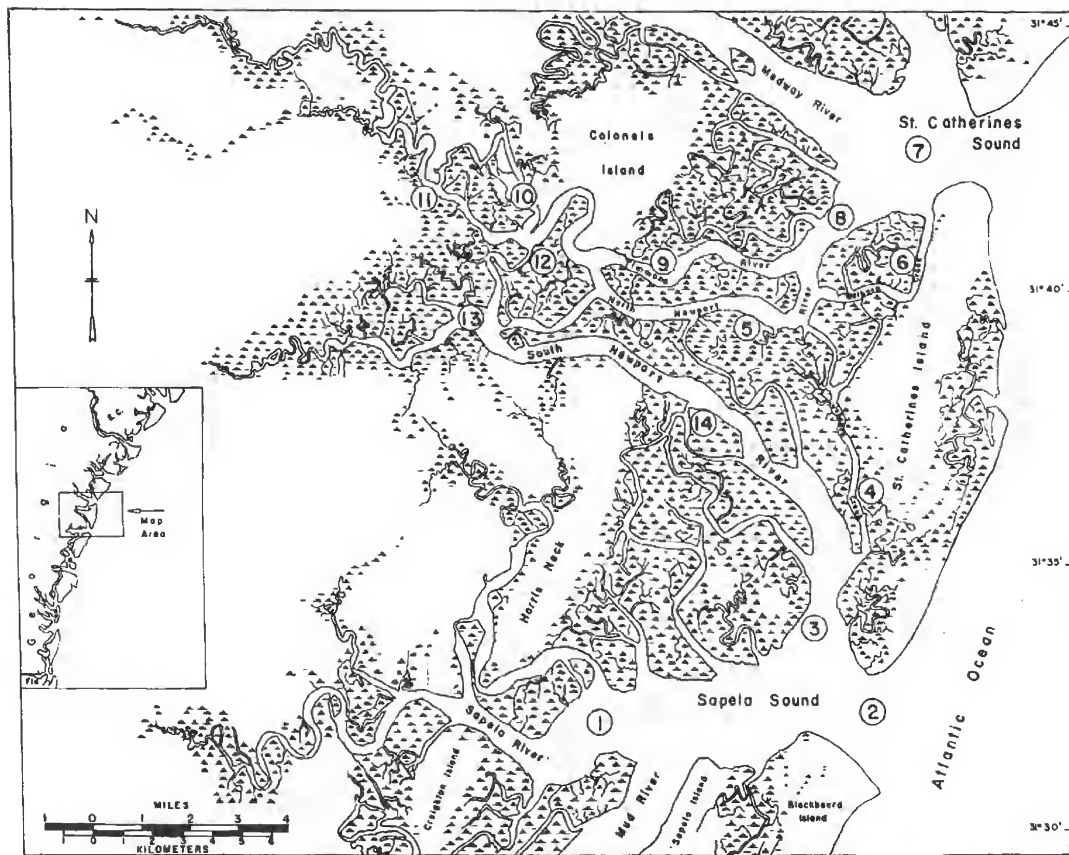
Figure 3. Map of Sapelo and St. Catherines Sounds indicating locations of 14 sites visited monthly during 1967 through 1970 for collections (bucket trawl and dredge) and water-quality data (from Sikora et al. 1972).

RESULTS AND OBSERVATIONS

Sapelo Island

A total of nine shell pairs and 25 single valves of *Mya arenaria* were found on seven occasions from July to December 1971 (Table 1) at the High Point River culvert site. All shells were thin and fragile. Although no living specimens were obtained, all shells had fresh periostracum. The attached tissue remnants on a few of the valves suggested that the living clams had been eaten by crabs, birds, or raccoons. The thin shells may be a result of life under less than optimal conditions for the species. All shells were found on the bottom of the pool on the landward side of the culvert and probably were washed in from the marsh by the

strong currents at high tide. The largest number of shells was found on 6 December, shortly after a strong storm on 2-3 December which raised the normal sea level over a meter. Water temperatures at the time of sampling ranged from high averages of 26.0-27.4°C in summer to low averages of 13.4-16.4°C in winter. Salinity ranged from 20-26°/oo in June and December to occasional lows of 3-5°/oo in August and in January-February which were associated with heavy local rainfall.

Despite careful and regular searches during the senior author's stay on Sapelo Island, no living specimens of *Mya arenaria* were found along the more open mud bars, beaches and sandy shallows of the island. Only a single valve of a dead and worn specimen, perhaps a fossil, 66 mm long, was found washed ashore on the open Atlantic beach.

TABLE 1

Mya arenaria from Sapelo Island, Georgia. Shells and attached shell pairs found in 1971. Shell length expressed as average (minimum-maximum); for averages, each shell pair counted as one unit.

Date in 1971	Shell Pairs	Single Shells	Shell Length (mm)	
9 July	2	--	29	(23-35)
8 September	1	--	48	
9 November	1	3	36.5	(34-39)
22 November	--	2	37	(36-38)
6 December	4	9 left, 5 right	40.7	(26-55)
20 December	--	2 right	35.5	(29-42)
27 December	1	3 left, 1 right	37.4	(30-47)

Of the many ditch and creek habitats of the island examined in 1971, only the above locality contained material of *Mya arenaria* in the form of fresh shells, some with tissue remnants. An attempt was also made to sample the *Spartina* marsh downstream from the drainage culvert, but the dense tangle of blades and rhizomes combined with the very soft mud made it nearly impossible to dig there. No living clams or recent shells were found. Since the possible uniqueness of this drainage ditch habitat was not known to us at the time, no further efforts were made to find living specimens.

We did not have an opportunity to collect in the channel bottoms of the adjacent tidal creeks (Post Office and Barn Creeks) on Sapelo Island where sand-silt substrata are present some sections of their runs. In future studies, such creek-bottom habitats should be sampled seasonally with cores, yabby pumps (hand-held suction devices), or small water-jet pumps to determine if softshell clams are present.

North Newport River

Our observations on North Newport River populations of *Mya arenaria* represent an expansion of the data presented in an unpublished final report by Heard and Heard (1971). In that study, which dealt with an ecological evaluation of the invertebrate communities in St. Catherines and Sapelo Sounds and their respective tidal river tributaries, *M. arenaria* was reported in bucket-dredge samples taken at three stations on eight different occasions. Softshell clams were reported at stations 10 and 11 from the middle, mesohaline reaches of the North Newport River during winter and spring (February to June) of 1969 (Table 2).

With the exception of salinity-temperature-DO measurements, neither Heard and Heard (1971) nor another unpublished companion report by Dahlberg (1971) presented exact information about depth and bottom conditions or the size and quantity of animals, whose occurrence was simply designated as "present," "common," or "abundant".

We are now able to present additional information on the populations of *Mya arenaria* collected from the North Newport and South Newport River systems during the 1967-1971 paper mill environmental impact study, but not included in Heard and Heard (1971). This information includes additional environmental data on the stations where softshell clams occurred, records from Station 12 (Table 2), and data on *M. arenaria* from the stomach contents rays and hakes.

During the five-month period in which *Mya arenaria* was present in the samples (10 February-2 June), temperatures at stations 10, 11, and 12 were lowest on 6 March (10.8°C at 10 and 11, 10.7°C at 12) and highest on 2 June (29.4°C, 28.1°C, and 28.3°C at 10, 11, and 12, respectively). Salinities for stations 10, 11, and 12 were lowest on 1 April (15.7⁰/oo, 12.4⁰/oo, and 15.3⁰/oo) and highest on 10 February (23.4⁰/oo, 23.6⁰/oo, and 25.4⁰/oo, respectively).

During the winter and spring of 1969, specimens of *Mya arenaria* were taken twice at station 10 ("present" in March and May) and five times at station 11 ("common" in February and April, "present" the other three months), and once at station 12 (station 12 not included in Heard and Heard 1971).

Regrettably, most of the specimens of *Mya arenaria* reported in Heard and Heard (1971) are now unavailable for study. However, voucher specimens for four of these eight North Newport River collections are extant. Stations, collection dates, and measurements for these voucher specimens are presented in Table 2.

TABLE 2

Occurrence of *Mya arenaria* collected with a bucket dredge from the North Newport River at stations 10 and 11 during March, April, May, and June 1969 (from Heard and Heard 1971), plus data from station 12 and from voucher specimens. Length measurements in mm for available voucher specimens.

Station (Cruise)	Date (1969)	No. of Clams	Shell Length mm*
10 (33)	1 April	present	unknown
10 (35)	2 June	present	unknown
11 (31)	10 February	(6) common	16.7 (14.2-20.6)
11 (32)	6 March	(8) present	17.7 (11-23.2)
11 (33)	1 April	(4) present	16.9 (14.2-20.6)
11 (34)	1 May	present	unknown
11 (35)	2 June	present	unknown
12 (32)	6 March	(2)	15.1 (8.1-22.1)

*Based on range and average of voucher specimens (number of voucher specimens in parentheses).

The voucher specimens from the February, March, and April collections appear to be juveniles and subadults. Based on notes and sketches of the second author, the specimens taken with the bucket dredge at Station 11 during June 1969 were distinctly larger than those collected in February and April (R. Heard, unpublished observations). These tentative observations are supported by the similar size (40+ mm) of softshell clam specimens taken from the stomachs of Atlantic stingrays collected at this station during the same period.

Fauna Associated with North Newport River *Mya arenaria* Populations

A fairly diverse benthic assemblage of macro-invertebrates was associated with spring populations of *Mya arenaria* in the North Newport River (Heard and Heard 1971). At stations 10, 11, and 12 in depths ranging from 4 to 8 meters, dense populations of the ascidian *Mogula manhattensis* (DeKay) with associated hydroids, bryozoans (*Anguinella palmata* van Beneden and *Amathia distans* Busk) and gammarid amphipods (*Gammarus mucronatus* Say and *Melita nitida* Smith) were attached to the consolidated pleistocene deposits along the edges of channels. Other species commonly associated with the pleistocene deposit community were the nereidid polychaete *Neanthes succinea* (Frey and Leuckart); the hooked mussel *Ischadium recurvum* (Rafinesque); the false angelwing *Petricola pholadiformis* Lamark; the common grass shrimp *Palaemonetes vulgarus* (Say); and the xanthid crab *Rhithropanopeus harrisii* (Gould).

In or on the sand-silt bottom deposits where *M. arenaria* occurred, three other mollusks were common: the Atlantic paper mussel, *Amygdalum papyrium* (Conrad), the dwarf surf clam, *Mulinia lateralis* (Say), and the brown banded wentletrap, *Epitonium rupicola* (Kurtz). Populations of the amphipod *Ampelisca abdita* Mills, the isopods *Cyathura polita* Stimpson and *Cleantoides planicauda* (Benedict), and the polychaetes *Diopatra cuprea* Bosc and *Sabellaria vugaris* Verrill also occurred in or on the same substratum with softshell clams.

Georgia Intertidal Populations of *Mya arenaria*

Additional observations on extant populations in Georgia waters were made by one of us (RWH) between 1962 and 1994. Ephemeral, intertidal, winter populations of juvenile *Mya arenaria* occurred intermittently on exposed pleistocene beach faces along Moon River, a mesohaline tidal river in Chatham, Georgia. In the lower intertidal zone along these shore faces, juvenile softshell clams (6-12 mm in length) were observed in small silt-filled depressions that pocked the consolidated sand-clay shore face. During some winters,

densities often exceeded 250 individuals per m^2. It is likely that such ephemeral juvenile "accessory" populations occur at other similar intertidal habits in Georgia estuaries during the winter and early spring.

Such juvenile clam populations may be bionomically important in the diets of shore birds. On several occasions during the late winter at the Chatham county site, flocks of small unidentified "sand pipers" were often seen feeding along the lower shore in areas where juvenile soft shell clams were common.

Possible Factors Determining the Occurrence of *Mya arenaria* in Georgia Estuaries

Based on our limited observations, Georgia populations of *Mya arenaria* appear to have restricted habitats, be most common during the winter and spring months, and have shell sizes that do not approach those found in northern softshell clam populations. Ecological factors, including salinity, food supply, substratum and temperature (Swan 1952a) determine the occurrence, distribution, and size of softshell clams in Georgia estuaries.

Salinity. Over the period of this study, salinity at the *Mya arenaria* collection site on Sapelo Island varied from highs of 20-26^0/oo in June and December to occasional lows of 3-5^0/oo in August and in January-February. Since *M. arenaria* is known to tolerate sudden and considerable changes in salinity (Matthiessen 1960), it is unlikely that the infrequent salinity fluctuations at the Sapelo Island site and those observed in the North and South Newport River systems would be a decisive factor in softshell clam survival.

Substratum. Theroux and Wigley (1983) found softshell clams to be most common in sand-silt bottoms. Swan (1952b) reported that these clams grow faster in sandy bottoms than in compact mud substrata. The substratum surrounding the ditch collection site was soft mud or mud permeated with rhizomes of associated marsh grasses. Based on the observations of Swan (1952a), softshell clam growth in this type of habitat may be retarded. This might be one reason why the largest shells examined from the extant population on Sapelo Island (Table 1) were only 4.8 cm long.

The largest specimens of *Mya arenaria* observed from the North and South Newport River systems were taken from stingray stomachs at station 11 during June 1969. Like clams from the Sapelo Island site, these clams had maximum valve lengths under 5 cm, even though the bottom sediments in the vicinity of this station were predominantly sand-silt and appeared to be more suitable for growth of softshell clams than the mud bottom at the Sapelo Island site.

Food supply. In Georgia habitats, food supply should not be limiting in view of the high primary production throughout the surrounding marsh and estuarine waters (Odum 1961). Odum and de la Cruz (1967), working on Sapelo Island, found the amount of organic detritus (2-20 mg ash-free dry organic matter per liter), mainly from *Spartina*, to be much greater than that reported for the open sea. The nutrient-rich waters of Georgia estuaries support a rich planktonic and benthic diatom flora (Pomeroy et al. 1981) which could be utilized as a food source by local populations of *Mya arenaria*.

Temperature. *Mya arenaria* is essentially a boreal-cold temperate species with its main distribution in more northern latitudes. Its restricted occurrence in the warm-temperate, estuarine waters of Georgia would be an interesting subject for studies on physiological adaptation. A comparison between the lower temperature conditions at the Sapelo Island drainage site that supported a population of *M. arenaria* during 1971 and the higher temperature conditions of adjacent marine habitats lacking clam populations may explain this special occurrence. Published hydrographic data from comparable habitats in Georgia coastal waters are mostly limited to hydrographic and ecological studies conducted in the sounds and oceanic waters adjacent to Sapelo Island. For comparison with the data from the brackish-water ditch habitats, we utilized physical data collected between 1967 and 1970 from surface waters at station 2 (Figure 3), located in Sapelo Sound off the northern tip of Sapelo Island (Dalhberg 1971). During that study, temperatures ranged from high averages of 28.7-29.2°C in summer to low averages of 8.8-11.8°C in winter. In spite of the fragmentary and incomplete data from both localities, these data suggest that overall lower temperatures exist at the drainage ditch site (13.4-16.4°C winter lows to 26.0-27.4°C summer highs) as compared to the open water (i.e., Sapelo Sound site), especially during the summer months. The subtle temperature differences in such specialized habitats that support lower temperatures during the summer months may help support a niche in which softshell clam populations can survive at lower latitudes where they normally would not be expected to survive.

High temperatures are reported to be an important limiting factor for softshell clams in southern estuarine habitats (Laursen 1966). Accordingly, well established populations of *Mya arenaria* normally occur in estuarine and marine habitats where water temperatures are consistently less than 28°C (Kennedy and Mihursky 1971). In Chesapeake Bay, large-scale mortalities of softshell clams took place when summer temperatures exceeded 28°C (Pfitzenmeyer 1972).

Temperature may also control the size of southern softshell clam populations. The observed small size of *Mya arenaria* specimens from Georgia estuaries may be an adaptive or ecophenotypic response to the overall higher temperatures found in southern parts of its range. As in southern populations of the Atlantic surf clam, *Spisula solidissima* (Dillwyn, 1817), Georgia estuarine softshell clam populations may mature at a smaller size and never approach the size of the northern "cold water" forms. It would be very interesting to culture transplanted juvenile specimens of *M. arenaria* from Georgia populations in a suitable New England habitat in order to determine if regional size differences are due more to environmental than to genetic factors.

In the cold temperate coastal habitats of New England where softshell clams are harvested commercially for food, shells are reported to commonly reach lengths of up to 7.6-15.4 cm (Abbott 1986). The largest known shell for *Mya arenaria*, collected at Barnstable Harbor, Massachusetts, has a length of 16.6 cm (Clench 1961). There also remains the possibility that adult clams of "typical" size (8+ cm) occur in Georgia waters, but have not been detected because of the limited and inadequate sampling methods employed thus far.

Softshell Clams in the Diet of Georgia Estuarine Fishes

Softshell clams occurred in the stomach contents of fishes collected in monthly trawls taken in the North and South Newport River during 1969 as part of a paper mill monitoring study (Dahlberg 1971). There is also an additional record of *Mya arenaria* from the stomach of an Atlantic stingray collected in June 1972 by trawl in a mesohaline area near the mouth of the Little Ogeeche River, Chatham Co., Georgia (R.W. Heard, unpublished data).

As part of a study on the feeding habits of the Atlantic stingray, *Dasyatis sabina* (Lesueur), collections were made during 1969 in the North and South Newport River systems when softshell clams occurred in benthic samples. It was found that *Mya arenaria* was an important part of the spring diet of the stingrays occurring in this area.

Between 1967 and 1972, the stomach contents of 321 Atlantic stingrays from a variety of Georgia coastal habitats were examined (R. Heard, unpublished data). Of these rays, 14 (5%) of the 293 rays with recognizable food in their stomachs had been feeding on *Mya arenaria* (Table 3). Of these 293 rays, 46 were collected from stations 10, 11, 12, and 13 in the North and South Newport River systems where known or suspected populations of softshell clam occurred during 1969. Of the rays examined from these stations on a year-round basis, 13 (28%) had been feeding on softshell clams. Based on examination of 26 rays collected during the spring from these stations, 50% contained from 2 to 17

softshell clams, which in terms of biomass comprised the major part of their diet. The majority of rays found feeding on *M. arenaria* occurred at station 11 during May and June 1969, where 11 of 13 (85%) of the stomachs examined contained clams. During the June collections, many of the softshell clam remains from the ray stomachs appeared to have valve lengths in the 30 mm to 40+ mm range. The remaining 20 rays examined from Stations 10-13 were collected during the fall months. They had been feeding predominantly on the commercial white shrimp, *Penaeus setiferus* (Linné), and had no softshell clams in their stomach contents.

Two small softshell clams were taken from the stomach of a juvenile spotted hake, *Urophycis regius* (Walbaum), collected during the spring of 1969 from the North Newport River above station 11 (Station C of Heard 1975). These two clams were in poor condition and are no longer available for study (Sikora, unpublished data; Sikora et al. 1972, footnote p. 518).

In another study (Heard 1975) which deals with the feeding habits of white catfish, *Ictalurus catus* (Linné), collected from the North Newport River and its tributaries, no *Mya arenaria* were observed in the stomach contents of 174 fish examined. Many of these catfish were collected at stations C and B (= station 11) during periods when softshell clams were known to be present.

Other Cold Temperate-Boreal Species in Georgia Estuaries

During the spring and winter months, the Baltic macoma, *Macoma balthica* (Linné, 1758), and the Atlantic rock crab, *Cancer irroratus* Say, 1817 occur in Georgia estuaries. Like *Mya arenaria*, both are common to cold-temperate and boreal Atlantic regions. *Macoma balthica* has been reported in Georgia waters (Abbott 1974; Theroux and Wigley 1983; Mayou and Howard 1975; Frey et al. 1975). Juveniles of the crab *Cancer irroratus* are not uncommon in the sounds near Sapelo Island (Heard and Heard 1971). *Macoma balthica* appears to be an important component of winter brackish water benthos of Doboy and Altamaha Sounds, which are part of the greater Altamaha River delta system just south of Sapelo Island (Mayou and Howard 1975; R.W. Heard, unpublished observations). The juveniles of *C. irroratus* are common winter residents of the lower, high salinity reaches of Georgia sounds. Adult populations south of North Carolina are confined to colder deep-water habitats (Williams 1984). Juveniles of *C. irroratus* have been reported in the diet of hakes collected in Sapelo and St. Catherines Sounds (Sikora et al. 1972). Juvenile hakes, like *C. irroratus*, occur in Georgia estuaries during the cooler periods of the year, and leave the estuaries during the spring to migrate back into deep offshore waters where the adult populations occur.

TABLE 3

Occurrence of *Mya arenaria* in 14 stomachs of the Atlantic stingray, *Dasyatis sabina*, collected from Georgia estuaries during 1967-1970 (North and South Newport River system) and 1972 (Little Ogeeche River).

Collection Date	Station	Disk Width (cm)	Sex	No. of *Mya* in Stomach
	North Newport River			
5/69	11	24	Female	5
	11	24	Female	5
	11	25	Female	3
	11	26	Female	17
	11	32	Female	14
6/69	11	21	Female	2
	11	26	Female	2
	11	29	Female	5
	11	30	Female	10
	11	30	Female	12
	11	33	Female	16
	South Newport River			
5/69	13	33	Female	4
	13	33	Female	15
	Little Ogeeche River			
6/72	17	23	Male	12

CONCLUSIONS

Based on our limited data, we believe that there is a good possibility that year-round, reproducing populations of the softshell clam, *Mya arenaria*, exist in Georgia waters. During the colder months, juvenile populations are often recruited into areas such as intertidal sand banks. During warmer months, however, biotic and abiotic factors such as predation and temperature may make these areas uninhabitable for the clams and thus limit their distribution.

The restricted cooler habitats associated with tidal ditches on Sapelo Island and the mesohaline tidal river channels with sand-silt bottom substrata like those associated with the middle reaches of the North and South Newport Rivers may serve as year-round refuges for local breeding populations of *Mya arenaria*. However, since Theroux and Wigley (1983) have documented that softshell clams occur at depths of over 150 m off New England, it is possible that permanent, offshore populations may be present on the continental shelves of the Carolinas, Georgia, and

northeastern Florida. Hypothetically, if such a situation exists, then the softshell clams from Georgia estuaries could simply be ephemeral, non-breeding accessory populations representing a seasonal larval recruitment from offshore populations. To our knowledge, however, no populations of *M. arenaria* are documented or known from the continental shelf off Georgia or immediately adjacent states.

Notwithstanding, softshell clams appear to be a bionomically important component of some Georgia estuarine habitats during winter and spring months. Further studies are needed to establish with certainty whether or not year round breeding populations of *Mya arenaria* exist in Georgia estuarine waters.

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Levinseniella deblocki, New Species (Trematoda: Digenea: Microphallidae) from Salt Marshes along the Eastern Gulf of Mexico with Notes on Its Functional Morphology and Life History

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LEVINSENIELLA DEBLOCKI, NEW SPECIES (TREMATODA: DIGENEA: MICROPHALLIDAE) FROM SALT MARSHES ALONG THE EASTERN GULF OF MEXICO WITH NOTES ON ITS FUNCTIONAL MORPHOLOGY AND LIFE HISTORY

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ABSTRACT *Levinseniella* (*Austromicrophallus*) *deblocki*, n. sp., was collected during parasitologic studies of homeothermic vertebrates from salt marshes along the coast of the eastern Gulf of Mexico. Because *L. deblocki* lacks a female pouch, it belongs to the subgenus *Monarrhenos* proposed by Deblock and Pearson (1970). However, since Deblock and Pearson did not explicitly designate a type species for *Monarrhenos*, it is not available and is a *nomen nudum*. The next available name, *Austormicrophallus* Szidat, 1964, a genus synonymized with *Levinseniella* Stiles and Hassall, 1901 by Deblock (1978), is reinstated as a subgenus to receive the species lacking a female pouch and previously assigned to *Monarrhenos*. The adult of *L. deblocki* is found in the lower digestive tracts of the clapper rail (*Rallus longirostris*), rice rat (*Oryzomys palustris*), and raccoon (*Procyon lotor*). Morphologically, *L. deblocki* appears to be most similar to *L. polydactyla* Deblock and Rosé, 1962, known from Europe, and *L. ophidea* (Nicol, Dameree, and Wootton, 1985), described from a freshwater habitat in California. Differences in the life cycle, habitat type, and geographic distribution, plus a combination of distinctive morphological characters (presence of lappets on the oral sucker, number of genital pockets, and body size) separate *L. deblocki* from the other members of the subgenus *Austromicrophallus*. The metacercarial stage of *L. deblocki* occurs in the gonads of fiddler crabs (*Uca* spp.) and the first intermediate host appears to be a hydrobiid gastropod (*Heleobops* sp.). Observations on living and preserved specimens fixed *in copula* indicate that the genital atrium functions as an eversible hermaphroditic organ bearing the male papillae and metraterm. The genital hooks or "Jägerskiöld's bodies" appear to function as holdfast structures during copulation.

INTRODUCTION

During parasitologic studies of homeothermic vertebrates from salt marshes along the coasts of the northeastern and southeastern Gulf of Mexico, we discovered an undescribed species of the microphallid genus *Levinseniella* Stiles and Hassall, 1901. The adult stage of this species occurred in the lower digestive tracts of clapper rails, rice rats, and raccoons. The new species appears to be most closely related to *L. polydactyla* Deblock and Rosé, 1962, known from Europe, and *L. ophidea* (Nicol et al., 1985), described from a freshwater habitat in California.

MATERIALS AND METHODS

Living and fixed specimens of excysted metaceriae from fiddler crabs (*Uca* spp.) and adults from naturally and experimentally infected vertebrate hosts were examined microscopically. Specimens were killed in hot saline with and without coverslip pressure, then immediately fixed in AFA, stained in Erlich's hematoxylin, dehydrated, cleared, and mounted in Permount (TM).

Living metacercariae were excysted in saline-typsin solution at 39°C; excystment usually occurred within 12 hours. Copulating pairs of worms were obtained by placing 50 to 100 excysted metacercariae together in warm saline (39°C). Copulating pairs were examined alive or were heat-killed in hot saline and fixed in AFA (with or without coverslip pressure). Some of the fixed copulating pairs were separated for stained slide preparations, while others were mounted still *in copula*. A Wild-20 drawing tube (camera lucida) aided in the preparation of the illustrations. All measurements are in micrometers (m).

Type material (holotype and paratypes) are deposited in the National Parasite Collection of the US National Museum (USNM), Beltsville, Maryland. Additional paratypes are in the collections of the Museum of the Gulf Coast Research Laboratory (GCRL).

RESULTS: TAXONOMY

Genus *Levinseniella* Stiles and Hassall, 1901

Synonyms. *Austromicrophallus* Szidat, 1964. *Heardlevinseniella* Yamaguti, 1971.

Subgenus *Austromicrophallus* Szidat, 1964, n.comb

Synonym. *Monarrhenos* Deblock and Pearson, 1970 (p. 784) *Nomen nudum.*

Diagnosis. Species of *Levinseniella* lacking a female pouch.

Type species. *Levinseniella* (*Austromicrophallus*) *anenteron* Szidat, 1964.

Other species referred to *Austromicrophallus*: *L. pellucida* Jägerskiöld, 1907; *L. amnicolae* Etges, 1953; *L. Polydactyla* Deblock and Rosé, 1962; *L. byrdi* Heard, 1968(a); *L. hunterae*[1] Heard, 1968(b); *L. monodactyla* Deblock and Pearson, 1971; *L. capitanea* Overstreet and Perry, 1972; and *L. ophidea* Nicol, Damaree, and Wootton, 1985; *L. ucatanensis* Camaris and Ching, 1989.

Heard (1968) divided the genus *Levinseniella* into four groups based on the presence or absence of a female pouch and the relative number of atrial pockets ("male pockets" of some authors) present. Deblock and Pearson (1970) proposed the subgenus *Monarrhenos* to receive the species of *Levinseniella* that lack a female pouch. They did not, however, explicitly designate a type species or give a bibliographic reference to a proposed type species for their "new subgenus" as required under Article 13 of the International Code of Zoological Nomenclature. Therefore, *Monarrhenos* cannot be considered an available name and is a *nomen nudum.* In his 1971 treatise, which was in press when Deblock and Pearson's 1970 paper designating the subgenus *Monarrhenos* was published, Yamaguti described the monotypic genus *Heardlevinseniella* to receive *L. byrdi* Heard, 1968. He characterized this genus by the absence of a female pouch and the presence of a postoral muscular ring and oral lappets. Because there are several other species that lack a female pouch (Heard's Groups III and IV), have a large oral sucker, and have a "postoral muscular ring," Overstreet and Perry (1972) synonymized *Heardlevinseniella* with *Levinseniella.* Deblock (1978) redescribed *Austromicrophallus anenteron* Szidat, 1964, a poorly-known monotypic species from gulls collected along the coast of Patagonia (Szidat, 1964). Based on the presence of atrial pockets and the absence of a female pouch, Deblock (1978) synonymized the monotypic *Austromicrophallus* Szidat, 1964 with *Levinseniella* and placed *A. anenteron* in *Monarrhenos.* Thus *Austromicrophallus* Szidat, 1964 is the oldest subgeneric

name available for those species lacking a female pouch and assigned to *Monarrhenos sensu* Deblock and Pearson (1970). *Levinseniella anenteron* and *L. capitanea* are both characterized by the absence of digestive ceca. Following Overstreet and Perry (1972) and Deblock (1978), we consider the absence of digestive ceca to be a highly derived character not warranting generic or subgeneric standing on its own.

Levinseniella deblocki, new species
Figure 1 A-G.

Synonyms. "*Levinseniella* sp. 2 (Heard, comm. écrite)": Deblock and Pearson (1971, p. 787; "*Levinseniella* sp. 2 (Heard, communicaion écrite)": Deblock (1971, p. 449); "*Levinseniella* sp. 2 (Heard In: Deblock and Pearson, 1971)": Nicol *et al.* (1985, p. 182); *Levinseniella* sp. A: Heard (1976, pp.83-98); *Levinseniella* sp.: Kinsella (1988, pp. 276, 277); *Levinseniella* sp.: Forrester (1992, [in part], p.95, 189).

Description (based on 10 mature worms). Body elongate, 777 to 1020 long by 220 to 278 wide in posterior third of body. Tegument spinose; spines becoming smaller and less conspicuous posteriorly, completely embedded in hindbody tegument. Oral sucker subterminal with well-developed ventrolateral papillae (lappets). Postoral muscular ring immediately posterior to oral sucker. Prepharynx 34 to 62 long. Pharynx 47 to 56 long by 43 to 47 wide. Esophagus 136 to 212 long. Cecae well developed, extending posterolateral and ending near lateral margins of body at level of acetabulum. Acetabulum recessed, 75 to 98 long by 63 to 93 wide. Forebody 63 to 73% of body length.

Testes immediately posterior to acetabulum, symmetrical, usually wider than long; right testis 38 to 67 long by 57 to 78 wide; left testis 44 to 58 long by 67 to 95 wide. Seminal vesicle-pars prostatica complex surrounded by thin membrane, retort-shaped, located intercecally immediately anterior to acetabulum; seminal vesicle 115 to 155 long by 46 to 75 wide; pars prostatica thick walled, 60 to 75 long by 42 to 50 wide, surrounded by numerous prostatic cells. Male genital papilla a relatively small blunt cone, 28 to 32 long by 28 to 30 wide at base, penetrated at base by ejaculatory duct, sperm duct opening at its tip. Genital pockets sinistral to genital pore, 8 to 14 in number; embedded in wall of eversible genital atrium; atrium, when not everted, with male papilla just under upper margin of genital pore; everted atrium protrudes through dilated genital pore, forming large large papilla-like structure, 95 to 110 in diameter (Figure 1, B-E).

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[1] Originally, Heard (1968b) named this species for Wanda S. Hunter, but incorrectly gave it the masculine ending "i" instead of the feminine "ae."
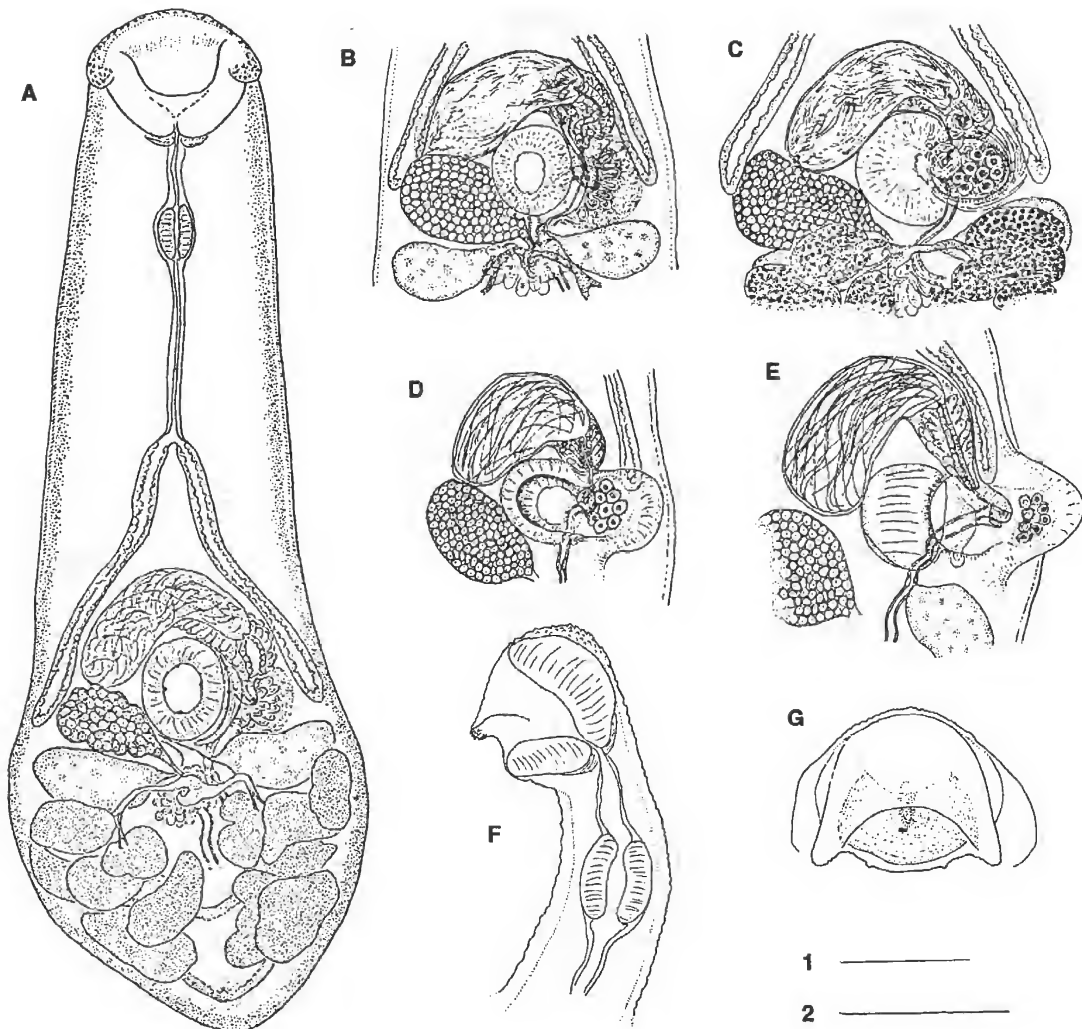
Figure 1. *Levinseniella deblocki,* n.sp.- A, ventral view of entire, mature worm; B-E, ventral views of ventral mid-region of body illustrating acetabulum and associated terminal genitalia. B, hermaphroditic organ retracted, genital pore not dilated; C, genital pore dilated, hermaphroditic organ beginning to protrude from genital pore; D, hermaphroditic organ (everted genital atrium) completely protruded through genital pore; E, protruded hermaphroditic organ under coverslip pressure showing openings of male papilla and metraterm); F, lateral aspect of oral sucker, post oral ring, pharynx, and lateral lappets; G, apical view of specimen showing lateral lappets adjacent to oral sucker. Scales = 100 m, scale 1 for A-E, scale 2 for F and G.

Ovary immediately anterior to right testis, dextral to acetabulum, 57-73 long by 73-113 wide. Oötype, Laurer's canal, and Mehlis' gland located in intertesticular region. Vitellariapost-testicular, acinose, six to seven relatively large follicles on each side. Uterine loops not reaching anterior to testes. Metraterm beginning in intertesticular region, passing dorsally along sinistral side of acetabulum, opening into dorsal portion of genital atrium at base of male papilla. Eggs, 18 to 21 long by 11 to 13 wide.

Excretory bladder U-shaped; pore subterminal, dorsal. Flame cell formula $2[(2+2)+(2+2)]=16$.

Holotype (USNM 84540).

Paratypes. Paratypes: 1 specimen from *Rallus longirostris* (USNM 84541), 1 specimen from *Rallus longirostris* (GCRL 1338); 1 excysted metacercaria from *Uca panacea* (GCRL 1339).

Type host. *Rallus longirostris* Boddaert (clapper rail).
Site of infection. Intestinal ceca.

Type locality. Upper Tampa Bay (June 1965).

Mammalian hosts. *Oryzomys palustris*, rice rat (in large intestine); *Procyon lotor* (L.), northern raccoon (in large intestine).

Localities. Marco Island (Collier County), Florida (*P. lotor*); Cedar Key (Levy County), Florida (*O. palustris*).

Etymology. This species is named for Professor Stéphane Deblock in recognition of his many contributions to the study of the systematics and biology of the family Microphallidae.

Second intermediate hosts (*Uca* spp.). *U. longisignalis* Salmon and Atsaides - Little Dauphin Island (Mobile County), Alabama; Cedar Key (Levy County), Florida. *U. panacea* Novak and Salmon- Horn Island, Jackson County, Mississippi.- *U. pugilator* (Bosc)- Cedar Key, Florida (Kinsella, 1988).

Metacercaria. Cysts spherical, 350 to 450 in diameter (from naturally infected *Uca panacea* collected from salt marshes adjacent to Big Lagoon on Horn Island, Mississippi).

Site of infection. Gonads (testes and ovaries).

Taxonomic Remarks. The absence of a female pouch places *Levinseniella deblocki* into the new subgenus *Heardlevinseniella* and the absence of a female pouch coupled with more than five genital pockets ("male pockets") places it in subgroup IV of Heard (1968a). In addition to *L. deblocki*, four other species (*L. polydactyla* Deblock and Rosé, 1962; *L. hunterae*[2] Heard, 1968; *L. capitanea* Overstreet and Perry, 1972; and *L. ophidea* Nicol, Dameree, and Wootton, 1985) are presently referable to Heard's subgroup. *Levinseniella capitanea* differs from *Levinseniella deblocki* by the former's much larger size, more numerous genital pockets (11-21), and the absence of a pharynx and digestive ceca. Both ecological and morphological differences distinguish *L. deblocki* from *L. ophidea*. *Levinseniella ophidea* utilizes leeches as second intermediate hosts, frogs and snakes as definitive hosts, and occurs in freshwater stream habitats (Nicol, Demaree, and Wootton 1985). Morphologically, *L. ophidea* is distinctly larger than *L. deblocki* and lacks lappets on its oral sucker. The presence of a massive male papilla and the absence of a pair of well-developed ventrolateral lappets on the oral sucker of *L. hunterae* separates it from *L. deblocki*. *Levinseniella deblocki* appears to be most similar to *L. polydactyla*, described from the metacercaria stage in a

marine isopod (*Sphaeroma hoockeri* Leach) from France (Deblock and Rose 1972). It is distinguished from *L. polydactyla* by having an oral sucker with a pair of ventrolateral lappets, a well-developed postoral muscular ring, and a greater range in the number of genital pockets (8 to 14), compared with 10 to 12 in *L. polydactyla*.

OBSERVATIONS

Functional Morphology of the Terminal Genital during Mating

Observations on the possible function of the genital atrium, the acetabulum, and the genital pockets or "Jägerskiöld's bodies" were made on mating pairs of *L. deblocki*. Copulating pairs of worms were obtained by placing 50 to 100 excysted metacercariae together in warm saline (39°C). When these specimens were examined after 1 to 2 hours, usually 25% or more of them were found *in copula* .

Study of living and permanently mounted specimens *in copula* demonstrated that during copulation, the entire "genital atrium" everts to form a large hermaphroditic organ bearing the male papilla, the genital pockets and the opening of the metraterm (see Figure 1 B-E). When the hermaphroditic organ was everted, the acetabulum rotated 60 to 80° and partially retracted into the dextral wall of the body, leaving a deep cavity or "acetabular genital atrium" large enough for the insertion of the genital organ of the partner. During copulation, the acetabulum of each worm functions as a true genital sucker by attaching to the lateral wall of the partner's hermaphroditic organ. The genital pockets (Jägerskiöld's bodies) of each worm then partially evert and mesh with those of its partner. While *in copula*, the terminal genitalia of each worm lies immediately opposite that of its partner, allowing the male papilla of each worm to be inserted simultaneously into the opening of the other's metraterm, thus facilitating the exchange of sperm (cross-fertilization). Excysted worms maintained at 39°C in saline produced eggs within 24 hours.

Life History

The adult stage of *Levinseniella deblocki* appears to be a well-established parasite of both mammals and birds. Clapper rails serve as an avian host for *L. deblocki* along the Gulf Coast of Florida (Heard 1976). Although mammals have been experimentally infected with *Levinseniella* (see Bridgman et al. 1972), the occurrence of *L. deblocki* in rice rats and raccoons from salt marshes along the Gulf Coast of Florida established the first records of the genus in

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[2] Originally, Heard (1968b) named this species for Wanda S. Hunter, but incorrectly gave it the masculine ending "i" instead of the feminine "ae."

naturally infected mammals (Heard 1976; Kinsella 1988; Forrester 1992).

Information on the life cycle of *L. deblocki* is incomplete, but a hydrobiid (*Heleobops* sp.) from salt marshes on Horn Island, Mississippi, shed a microphallid cercaria that appeared to be its larva. In an experiment, this cercaria penetrated *U. longisignalis* and formed cysts in the gonads within 48 hours. Due to high mortality in the fiddler crabs used in this experiment, development to the mature metacercarial stage did not occur. The suspected cercaria of another microphallid *Gynaecotyla* sp. also occurs in *Heleobops* sp. from the same area. These two cercariae can be distinguished from each other by their stylet lengths. The stylet length of the *Levinseniella*-like cercaria was 17 m, whereas the stylet length of the *Gynaecotyla*-like cercaria was 22 m.

The infected fiddler crab and vertebrate hosts of *L. deblocki* occurred sporadically in the higher salinity salt marshes along the edge of the eastern Gulf of Mexico. The distribution pattern of these infected second intermediate and definitive hosts appears to be directly related to the presence of the suspected gastropod host, *Heleobops* sp.

DISCUSSION

A variety of malacostracan crustaceans, and in one instance a leech, have been reported to be the second intermediate hosts for species of *Levinseniella*. However, more detailed morphological and life history studies are needed, especially for species occurring in Eurasia, before many of these reports can be verified.

Amphipods and isopods have been reported as second intermediate hosts for several species of *Levinseniella* (Villot 1875; Etges 1956; Ouspenskaia 1960, 1963; Deblock and Rosé 1962; Reimer 1963; Rebecq 1964; Heard 1970, 1976; Galaktionov 1988; Galaktionov and Malkova 1993). Besides *L. deblocki*, several other species of *Levinseniella* are known to use decapods as second intermediate hosts (see Table 1).

TABLE 1

Decapod crustaceans reported as hosts of *Levinseniella*.

Species of *Levinseniella*	Second intermediate host(s)	Reference(s)
L. brachysoma sensu Balozet and Callot*	*Palaemonetes punicis*	Balozet and Callot (1939)
L. capitanea	*Callinectes sapidus*	Overstreet and Perry (1972)
*L. caracinides***	*Carcinides maenas*	Rankin (1939)
L. conicostoma	*Hemigrapsus penicillatus*	Bridgman et al. (1972), Kifune and Takao (1972)
L. cruzi sensu Mortonrelli and Shuldt	*Palaemonetes argentinus*	Martorelli and Schuldt (1990) Schuldt and Lunaschi [1985(1987)]
L. deblocki, n. sp.	*Uca longisignalis, U. panacea, U. pugilator, U. rapax*	Heard (1976) [as *L.* sp A], Kinsella (1988) [as *L.* sp.], present report
L. cf. pellucida sensu Nikitina	*Astacus lepodactylus eichwaldi*	Nikitina (1983)
Levinseniella sp.***	*Upogebia affinis*	Pearse (1945)
Levinseniella sp.	*Uca* sp.	Cable et al. (1960)
Levinseniella sp. C	*Rhithropanopeus harrisii*	Heard (1976)
Levinseniella sp.	*Portunus pelgicus*	Shields (1992)
Levinseniella sp.	*Pachygrapsus tansversus*	Bush et al. (1993)

*   Identification questionable (=*Spelotrema* sp.?)
**   Identification questionable (=*Spelotrema similis?*).
*** Generic designation questionable.

Some of the earlier reports of *Levinseniella* metacercaria in decapod crustaceans may be erroneous or need confirmation. Balozet and Callot (1939) reported the shrimp, *Palaemonetes punicis*, from Tunisian waters as an intermediate host of *L. pellucida*; however, Yamaguti (1958, page 886) questioned the identity of their material, indicating that it was probably a species of *Microphallus* Ward, 1901. After studying the description and figure given by Balozet and Callot, we concur with Yamaguti that the Tunisian specimens do not belong to the genus *Levinseniella*. Rankin (1939) suspected the green crab, *Carcinides maenas* (L.), to be the second intermediate host of *L. carcinides* Rankin, 1939, a species described from New England; however, this conjecture has not been confirmed. The metacercaria mentioned by him may have been *Microphallus similis* (Jägerskiöld, 1900), reported from the same crab host by Stunkard (1957). Cable (1956) mentioned the presence of *Levinseniella* metacercariae in fiddler crabs from Puerto Rico, but this record has not been confirmed. Pearse (1945), working at Beaufort, North Carolina, reported a trematode metacercaria from the anomuran mud shrimp *Upogebia affinis* (Say) which he tentatively identified as a species of *Levinseniella*. One of

us (RWH, unpublished data) examined over 100 specimens of this mud shrimp from the Beaufort area and found no microphallid metacercariae.

Levinseniella ophidea is the only species known to use noncrustacean second intermediate hosts. The metacercarial stage of this species was reported in four species of leeches from a California freshwater stream habitat (Nicol et al., 1985).

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Gulf Research Reports

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Pseudione overstreeti, New Species (Isopoda: Epicaridea: Bopyridae), A Parasite of *Callichirus islagrande* (Decapoda: Anomura: Callianassidae) from the Gulf of Mexico

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PSEUDIONE OVERSTREETI, NEW SPECIES (ISOPODA: EPICARIDEA: BOPYRIDAE), A PARASITE OF *CALLICHIRUS ISLAGRANDE* (DECAPODA: ANOMURA: CALLIANASSIDAE) FROM THE GULF OF MEXICO

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ABSTRACT Pseudione overstreeti, new species, is a common bopyrid that infests the branchial chamber of the beach ghost shrimp, *Callichirus islagrande*, occurring along beaches of the Gulf of Mexico from Cape San Blas, Florida to Paraiso, Tabasco, Mexico. Like other members of the genus *Pseudione* that infest callianassid shrimps, the female of *P. overstreeti* is characterized by biramous terminal appendages which result from the combination of uniramous uropods with the closely associated lateral plates of pleomere 6. From the other members of the genus *Pseudione* occurring on callianassid hosts, *P. overstreeti* is distinguished by the distinctive development of the coxal and lateral plates on the female and the presence of elongate, posterolateral processes (= uropods by previous usage) on pleomere 6 of the male. *Pseudione overstreeti* is the second bopyrid from a callianassid host in the northeast Atlantic. The other species, *Ione thompsoni* Richardson, 1904, described from New England waters, infests the branchial chamber of *Gilvossius setimanus* (DeKay, 1844).

INTRODUCTION

Over the past 15 years, we have collected specimens of the beach ghost shrimp, *Callichirus islagrande* (Schmitt, 1935), infested with an undescribed branchial bopyrid parasite. Parasitized ghost shrimp were collected using a suction devise or modified "yabbie pump" similar to that described by Manning (1975). Infested *C. islagrande* occurred in both intertidal and shallow subtidal habitats along sand beaches of the Gulf of Mexico. The description of this new species of bopyrid is the subject of this report.

The holotype has been deposited in the National Museum of Natural History (USNM), Washington, D.C. Paratypes are in the collections of the National Museum of Natural History, the Gulf Coast Research Laboratory Museum (GCRL), and the Museum National d'Histoire Naturelle (MNHN-Ep), Paris.

Pseudione overstreeti, new species
Figures 1 and 2
Pseudioniinae sp. A.: Rakocinski *et al.* 1993:102

MATERIAL EXAMINED
[ALL INFESTING *CALLICHIRUS ISLAGRANDE* (SCHMITT, 1935)]

HOLOTYPE, ♀ (USNM 253087); west end of Horn Island, Mississippi; 9 Oct 1981; 1 m water depth; coll. R.W.

Heard and D.L. Adkison. PARATYPES; **Mississippi:** 1♂ (USNM 253088), same collection as holotype; 2 ♀♀ (gravid), 2 ♂♂ NMHN-Ep. 876 (host present); west end of Horn Island; 05 Jul 1992; swash zone; coll. D.L. Adkison and R.W. Heard. 3 ♀♀ (gravid), 2♀♀ on same host, 3♂♂ (USNM 253089); west end of Horn Island; 01 Jun 1993; swash zone to 0.5m; coll. D.L. Adkison. 1♀ (gravid), 1♂, USNM 253090; Ship Island; no date; next to swash; coll. R.W. Heard. **Florida:** 1♀ (gravid), 1♂ (GCRL 1337); Panama City Beach (Bid-A-Wee Beach), Florida; 24 Oct 1990; 0.5 m; salinity 33 °/oo; coll. J. Foster. **Alabama:** 2♀♀ (gravid), 2♂♂ (USNM 253091); Gulf Shores; Oct 1980; 0.5 to 1.0 m; coll. R.W. Heard. 2♀♀ (gravid), 2♂♂ [double infestation]; west end of Dauphin Island; 08 Jul 92; swash zone; coll. D.L. Adkison. **Louisiana:** 1♀ (gravid), 1♂ (USNM 253092); Elmer's Island, Jefferson Parish; 21 Jun 1982; coll. R.W. Heard.

OTHER MATERIAL

Florida: 3♀♀ (gravid), 3♂♂ (1 double infestation); specimens deposited in GCRL Invertebrate Zoology Class Collection [apparently lost]; Cape San Blas, Florida; 28 June 1983, coll. R. W. Heard. 2♀ (1 gravid), 2♂ (USNM 253093); Perdido Key; 16 Jan 1990; swash zone and intertidal coll. R.W. Heard, C. Rakocinski and J.A. McLelland. **Alabama:** 1♀ (gravid), 1♂ (USNM 253094); west end of Dauphin Island; 30 Jun 93; swash zone; coll.
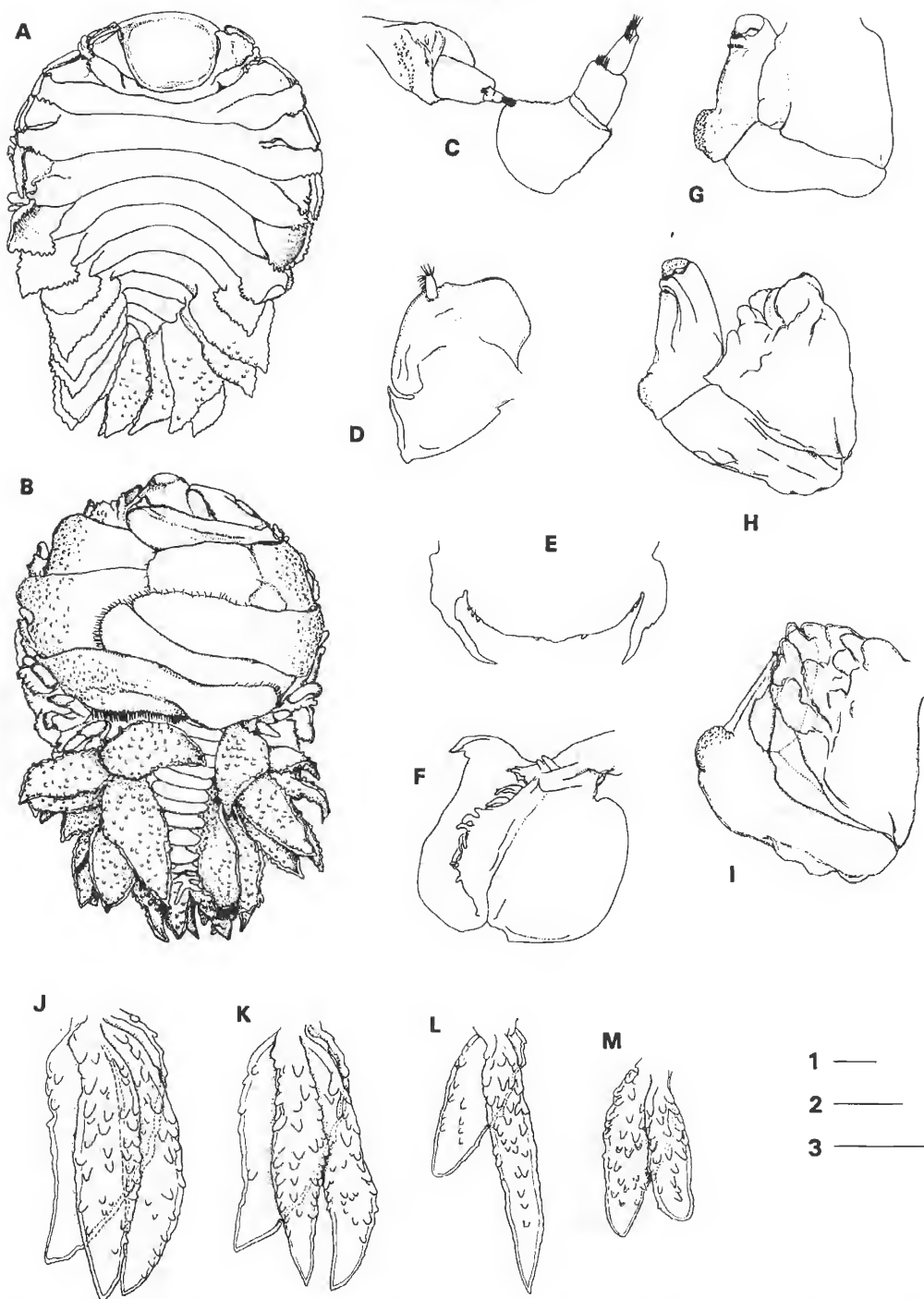
Figure 1. *Pseudione overstreeti*, new species. Female: A, dorsal view; B, ventral view, male shown attached to abdomen; C, antennae; D, maxilliped; E, posterior ventral lamina; F, oostegite 1, internal view; G, pereopod 3; H, pereopod 6; I, pereopod 7; J, pleopod 4; K, pleopod 5; L, left uropod and lateral plate; M, right uropod and lateral plate. Scale 1 = 0.1 mm (C); scale 2 = 5.0 mm (A and B), 1.0 mm (D-F, J-M); scale 3 = 0.5 mm (G-I).
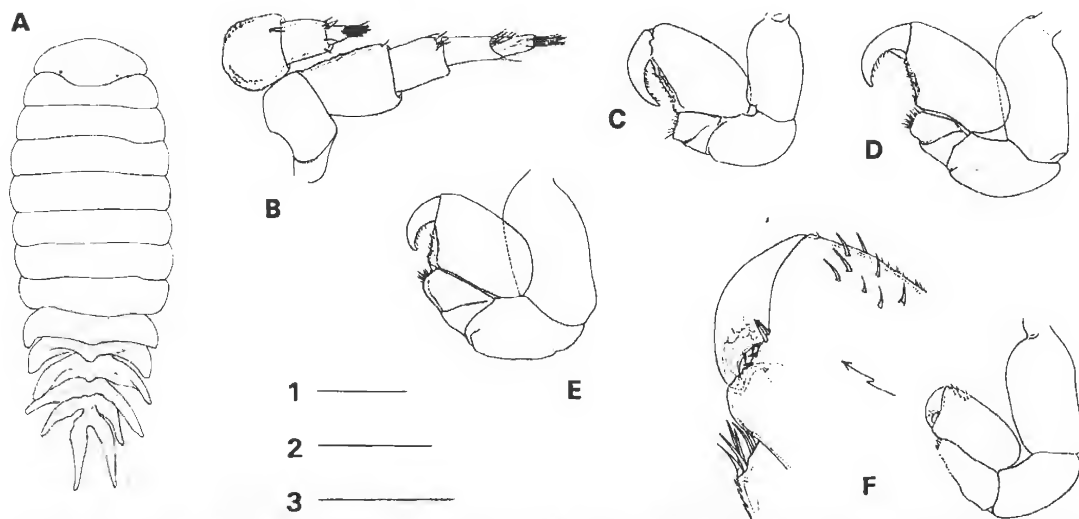
Figure 2. *Pseudione overstreeti*, new species. Male: A, dorsal view; B, antennae; C, pereopod 1; D, pereopod 3; E, pereopod 4; F, pereopod 7. Scale 1 = 1.0 mm (A); scale 2 = 0.2 mm (B); scale 3 = 0.4 mm (C-F).

D.L. Adkison. **Mississippi:** west end of Horn Island; 5 Dec 1980; 0.5 to 1 m; coll. R.W. Heard. 2♀♀ (gravid), 2♂♂ (USNM 253095); west end of Horn Island; 9 Oct 1981; 0.2 to 1.5 m; coll. R.W. Heard and D.L. Adkison. West end of Horn Island; 05 July 1992; coll. D.L. Adkison and R.W. Heard. **Louisiana:** 1♀ (gravid), 1♂ (USNM 253096); bay side of Isles Dernieres; coll. D.L. Felder; 24 Feb 1991. **Texas:** 5♀ (gravid), 5♂ (USNM 253097); Mustang Island, south of Port Aransas; 02 Aug 1990; coll. R.D. Felder and J.L. Stanton. **Mexico, Tabasco:** 2♀ (gravid), 2♂ (one damaged, without pleon) (USNM 253098); Paraiso; 28 Mar 1991; coll. D.L. Felder and J.L. Stanton.

DESCRIPTION

Female. Total length 10.0 to 19.1 mm; head width 3.0 to 6.5 mm; pereon greatest width (pereomere 3) 9.3 to 14.4 mm; pleon length excluding lateral plates 2.0 to 6.1 mm. Distortion angle 15°.

Head with dorsal surface nearly flat; frontal lamina narrow, laterally expanded, with margin often crenulate. Eyes absent. Antennule with 3 articles; covered with scales. Antenna with apparently 4 articles, articulation indistinct; more than twice length of antennule; covered with scales, more apparent than on antenna. Maxilliped palp often articulated indistinctly, with setae on distal and medial margins; maxilliped with numerous fine setae on ventral surface of distal segment. Barbula with 1 pair of unarmed lanceolate, lateral projections ("spur" of Adkison and Heard 1978 or "epipods" of Bonnier 1900), with numerous tubercles between lateral projections; tubercles shorter medially.

Pereon broadest at pereomere 3. Dorsolateral bosses on pereomeres 1-4; lateral margin with tubercles exhibiting variable development. Coxal plates free on pereomeres 1-4, fused with dorsolateral boss area on pereomeres 5-7; lateral and ventral surfaces tuberculate; tubercles most abundant on proximal ventral surface. Tergal area increasing in size to pereomere 4, then decreasing greatly posteriorly; tergal area on pereomeres 1-4 tuberculate posterolaterally; tubercles often present on pereomere 5. Brood pouch closed. Oostegite 1 with curved, medially directed posterolateral point; internal ridge armed with numerous long tubercles, becoming longer laterally; tubercles and internal ridge covered with scales. Oostegites 2-5 with tubercles on ventral surface in areas not overlapped by other oostegites; tubercles increasing in size proximally, often developed into ridge posterior to respective pereopod; size and area of tubercular coverage increasing on posterior oostegites; oostegite 5 with tubercles over most of ventral surface. Pereopods with basal carina, both increasing in size posteriorly.

Pleon short, width decreasing posteriorly. Uniramous lateral plates on pleomeres 1-6, lengths subequal, with tuberculate margins, dorsal surface without or with few tubercles, ventral surface with numerous tubercles, tubercles most abundant on anteroproximal region and often

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developed into ridge. Pleopods 5 biramous pairs, with rami similar in length, width decreasing posteriorly; rami with tubercles on both dorsal and ventral surfaces; with lateral margins having row of tubercles alternatingly directed dorsally and ventrally, with size and number of tubercles decreasing distally; tubercles most apparent on posterior pairs. Pleopods longer than associated lateral plates. Uropods uniramous, similar in appearance to associated sixth pair of lateral plates. Uropods and sixth pair of lateral plates superficially resembling biramous uropods (Figure 1 L,M).

Variation. Frontal lamina development variable, related to size of specimen, larger specimens usually more developed; tubercular development most variable on on barbula, internal ridge of oostegite 1, ventral area of oostegites 2-5, and to lesser degree on pleopods.

Male. Length without posterolateral elongation of pleomere 6 4.7 to 5.9 mm; width across pereomere 4 or 5 1.7 to 2.3 mm; pleon length at midline, excluding posterolateral elongations, 1.6 to 2.0 mm.

Head much narrower than pereomere 1. Eyes indistinct, represented by pair of minute pigment spots, often superficially indistinct. Antennule with 3 segments. Antenna with 5 or 6 segments, more than twice length of antennule. Maxilliped not seen.

Pereon compact without dorsal pigmented areas and lacking midventral tubercles; posterior pereomeres laterally distinct, separated from each other for greater part of width. Pereopods decreasing in length posteriorly, most apparent in dactylus and propodus.

Pleon with 6 pleomeres, with pleomeres separated for most of width, becoming produced laterally on posterior pereomeres; pleomere 1 relatively straight, laterally blunt; posterior pleomeres more elongate and directed more posteriorly. Pleopods vestigial or absent, represented by low mounds mesal to lateral processes of pleomeres when present, larger on anterior pleomeres. Pleomere 6 with posterolateral margins elongate and asymmetrically developed (superficially resembling uropods); uropods absent; anal cone with tubercle on posterodorsal surface.

Variation. Shape and relative elongation of pleomeres variable; posterior processes on pleomere 6 more robust and shorter than illustrated (Figure 2A) in some specimens (i.e., a male from Tabasco, Mexico), but lateral processes on pleomere 5 of most specimens tapered elongate projections like those illustrated in Figure 2A. Posterior pleomeres missing in several specimens, probably from host derived damage. Pleopod development and armature of antennae more pronounced in immature specimens than in adults.

Etymology. The species is named in honor of Robin M. Overstreet in recognition of his many contributions to the field of marine parasitology.

Distribution. *Pseudione overstreeti*, like its callianassid host, appears to be endemic to the Gulf of Mexico. It is presently known from Cape San Blas, Florida to Tabasco, Mexico.

Habitat. In branchial chamber of the beach ghost shrimp, *Callichirus islagrande*. Infected hosts have been collected in the intertidal zone to a depth of approximately two meters.

Remarks. The combination of strongly tuberculate posterior coxal plates and a pair of elongate terminal abdominal appendages formed by the combination of the uniramous uropods and lateral plates of last abdominal somite (sixth pleomere) distinguish the female of *P. overstreeti* from that of other nominal members of the genus *Pseudione*. The male, which lacks uropods and recognizable pleopods, differs from the other described species of the genus by the uniquely elongate, posterolateral margins of its sixth abdominal somite (Fig 2A).

Worldwide, numerous bopyrids are known to infest members of the Callianassidae; however, in the northwestern Atlantic only one other species, *Ione thompsoni* Richardson, 1904, is known. This species was described from *Gilvossius setimanus* (DeKay, 1844) (=*C. atlantica* Rathbun, 1926) collected in New England waters. *Pseudione overstreeti* and *I. thompsoni* belong to different subfamilies and are immediately distinguished by the development of the lateral plates on the pleon of the female. In *I. thompsoni*, the lateral plates are greatly branched and appear branchial in nature, while on *Pseudione overstreeti*, the lateral plates are simple tuberculate processes.

DISCUSSION

Within the Bopyridae, the number and type of appendages or projections on the sixth pleomere of the female have three interpretations: (1) the uropods are biramous (lateral plates absent); (2) the uropods are uniramous with lateral plates present; or (3) the lateral plates are biramous (uropods absent). At least two of these morphological conditions appear to have evolved in female bopyrids.

In the original description of *Pseudione longicauda* Shiino, 1937, a callianassid parasite from Japanese waters, Shiino (1937: 480) described the female as having uropods that are "uniramous on the left..[and] biramous on the right [,] branching at a short distance from the base." His illustration of the right uropod (p.481, Figure 2B) indicated a triramous structure composed of a biramous uropod and a lateral plate. The fifth pair of lateral plates on female of *P. overstreeti* appears to be similar to the unbranched right

uropod of *P. longicauda* as described by Shiino (1937: 480, Figure 1A). Later, Shiino (1958) examined the uropods of two additional adult females of *P. longicauda* and considered the uropods on these specimens to be uniramous. In the same study, however, he reported a juvenile female from the same collection as having a large exopod [lateral plate?] and a rudimentary endopod.

In *P. overstreeti*, the dorsal rami are similar in appearance to lateral plate 5, and the ventral rami are similar in appearance to the rami of pleopod 5. The lateral plates on pleomere 1-5 and the associated pleopodal rami are different in appearance. The pleopodal rami are more elongate than their respective lateral plates. The differences in structure of the pleopods and lateral plates of pleomeres 1-5 are similar to the differences between the dorsal and ventral rami of pleomere 6. Based on these observations, we consider the appendages on the sixth pleomere to represent a pair of lateral plates and a pair of more ventrally located uniramous uropods. The sixth female pleomere of *P. overstreeti* has two pairs of elongate projections, which we consider to be derived from the combination of a pair of uniramous uropods and a pair of lateral plates.

In male bopyrids, "uropods" have two forms. The first is derived from the posterolateral elongations of pleomere 6, and the longer the projections, the more likely they will be considered uropods (see Bourdon, 1968 and Markham, 1982). In the second form, the uropods are described as appendages with distinct proximal constrictions or articulations. In the male of the genera *Entophilus* Richardson, 1903, *Gigantione* Kossman, 1881, *Ionella* Bonnier, 1900, *Parapleurocryptella* Bourdon, 1972, and *Progebiophilus* Codreanu and Codreanu, 1963 (not *P. sinicus* Markham, 1982), the terminal appendages are proximally articulated or constricted. We consider these terminal appendages to be true uropods. Analogous structures arising from the posterolateral margins of the sixth abdominal somite lack any vestiges of a proximal constriction as seen in the male of *P. overstreeti*. These are terminal, lateral processes and not "true" uropods. The previous inexact usage of the term "uropod" for the appendages or processes on the posterior margin of the last pleomere has allowed two different, non-homologous structures to be referred to as the same. This situation causes problems in systematic studies, because within the Bopyridae, the presence of true uropods would be considered a plesiomorphic character and the presence of highly modified lateral processes would be considered an apomorphic character. For bopyrids, we strongly urge that the term "uropods" be reserved for those structures that are distinctly set off from the pleomere by an articulation or the vestige of an articulation.

Ecological notes. As in most other hosts having bopyrid infestations, reproductive activity in *C. islagrande* is suppressed by the presence of *P. overstreeti*. We examined over 100 specimens of *C. islagrande* parasitized with mature pairs of *P. overstreeti*, and all the hosts appeared to be females. These parasitized specimens had greatly reduced ovaries (Figure 3), and no ovigerous specimens were observed. Even when including hosts infested with juvenile or immature female *P. overstreeti*, only a single recognizable subadult male host was found, and it was parasitized by a juvenile female. In this male host, the first major chela was reduced and it appeared to be in transition to a female form. From our limited observations, we are unable to determine whether infestations occurred most commonly on primary females or if many of the hosts are female morphotypes derived from the metamorphosis of juvenile primary males infested with *P. overstreeti*.

We have observed double infestations on several occasions, with a female-male pair of *P. overstreeti* occurring in each host branchial chamber. In some instances, both females on the same host were gravid, but in all cases the females were of similar size and development.

Other symbionts, such as copepods (*Clasidium* sp.) and pinnotherid crabs (*Pinnixa behreae* Manning and Felder, 1989 in Alabama, Mississippi, and Louisiana waters) or *P. chacei* Wass, 1955 (in Mississippi, Alabama, and Florida waters), often co-occurred with hosts infested with *P. overstreeti*.

We also examined several hundred specimens of *Callichirus major* (Say, 1818) from populations co-occurring with those of *C. islagrande* infested with *P. overstreeti*. Although copepods and pinnotherid symbionts were present, we found no bopyrids on *C. major*.

Figure 3. A, photograph of unparasitized male (left) and female (right) of *Callichirus islagrande*; note orange ovaries seen through exoskeleton of the first two abdominal somites of the female. B, *Pseudione overstreeti*, new species, in right gill chamber of "female" *C. islagrande*.

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TROPHIC STRUCTURE OF MACROBENTHIC COMMUNITIES IN NORTHERN GULF OF MEXICO ESTUARIES

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ABSTRACT Trophic structure of estuarine benthic communities in the northern Gulf of Mexico was characterized according to the functional roles and geographic distributions of the macrobenthos. Macrobenthic organisms collected during two years of study were assigned to trophic groups to assess the relative utilization of detritus and other resources. Three groups of detritivores (surface-deposit feeders, subsurface-deposit feeders, and filter feeders) were numerically dominant among the benthos, each of which accounted for 25-30% of total abundance across regions. Carnivorous macrobenthos also comprised an appreciable portion (12%), while omnivores (<3%) and other groups (<4%) were poorly represented. Dominance by detritivores is consistent with current concepts regarding the role of macrobenthos in processing detritus of Gulf of Mexico estuaries.

INTRODUCTION

One of the central tenets of estuarine ecology is that organic detritus provides a major food source for estuarine benthic organisms (Darnell 1961; Day et al. 1989; D'Avanzo and Valiela 1990). Darnell (1961) was the first to study the role of detritus in Gulf of Mexico estuaries when he examined gut contents of consumers from Lake Pontchartrain, Louisiana (*vide* Day et al. 1989). Until recently, however, the scarcity of information on feeding biology of macrobenthic organisms prevented comprehensive studies of the trophic ecology (i.e., feeding ecology) of estuaries. Consequently, studies of the macrobenthic trophic ecology of northern Gulf of Mexico estuaries were lacking.

Several regional investigations of trophic structure were conducted recently to examine relationships between macrobenthic trophic structure and environmental gradients in Gulf of Mexico estuaries and nearshore waters (Flint and Kalke 1985, 1986a, 1986b; Gaston and Nasci 1988; Gaston et al. 1988, 1992; Gaston and Young 1992; Gaston and Edds 1994). These studies compared habitats or specific environmental characteristics of estuaries (e.g., salinity effects, contaminant effects), but were of limited geographic scope. By contrast, we compared estuaries on a broad geographical scale from Florida to Texas in order to examine variation in macrobenthic trophic structure and to assess the role of detritus and other resources. We also compared patterns of trophic structure observed in this study with those of previous studies.

METHODS

Sampling Design

Samples were collected from 201 estuarine stations (603 samples) from Anclote Anchorage, Florida to the Rio Grande River, Texas during July - August 1991 (100 stations) and 1992 (101 different stations) under the auspices of the U.S. Environmental Protection Agency Environmental Monitoring and Assessment Program (EMAP). A surface-area based, probabilistic sampling design was used to ensure that all estuarine "resource types" were equitably sampled and represented (Summers et al. 1992; Engle et al. 1994). Estuarine resource types included large estuarine systems (> 260 km²), small estuarine systems (> 2.6 km² but < 260 km²), and large tidal rivers (> 260 km² with aspect ratio > 20).

Sampling and Sample Analyses

Loran-C was used to locate sampling stations where water quality parameters were measured and quantitative benthic macroinvertebrate samples were collected (see methods in Heitmuller and Valente 1991; Summers et al. 1992). Three replicate macrobenthic samples were collected with a modified Van Veen grab (413 cm²). Samples were washed on a 500-μm screen, transferred to bottles containing 10% buffered formalin and Rose Bengal as a vital stain, and shipped for laboratory analysis.

Benthic samples were rewashed in the laboratory on a 500-µm screen, sorted to taxonomic groups for later identification and enumeration, and placed in labeled vials containing 70% ethanol. Ten percent of all sorted samples were resorted to ensure consistency and quality of work. When resorting revealed more than 10% error in removal of organisms, the previous ten samples completed by that sorter were reanalyzed. Organisms were identified to the lowest practical taxon and enumerated, and voucher specimens were compiled. Quality checks of identifications and counts were conducted by senior project taxonomists, and greater than 10% error resulted in reanalyses of samples. A complete description of quality assurance procedures used in this program is available in Heitmuller and Valente (1991) and Summers et al. (1992).

Macrobenthic Trophic Group Assignments

Each of the macrobenthic organisms identified during the study period was assigned to a trophic group based on feeding behavior and food type. Trophic groups used in this study were surface-deposit feeders (SDF), subsurface-deposit feeders (SSDF), suspension and filter feeders (FF), carnivores (CARN), omnivores (OMNI), and others (XXX) (*sensu* Gaston and Nasci 1988). Trophic group assignments were based on morphological and behavioral characteristics of estuarine macrobenthos supported by peer-reviewed scientific literature, unpublished observations, and personal expertise of the authors. Count data for species that fed by more than one method were evenly divided among the feeding groups assigned to that species (e.g., spionid polychaetes feed both on suspension matter and surface detritus; hence FF/SDF).

Data Analysis

Macrobenthic abundance data from 201 randomly selected base stations were used to estimate relative proportions of each trophic group found in estuaries of the northern Gulf of Mexico (i.e., Louisianian Province). This province-wide analysis was completed using data from randomly selected base stations for 1991 and 1992 combined, as well as for each sampling year independently. In addition to year-to-year comparisons, community structure was compared among four regions of the Louisianian Province. Regional comparisons were based on data from 86 stations (16 in Texas, 13 in Louisiana, 44 in Mississippi-Alabama, 13 in Florida) that represented five estuaries in each region, selected *a priori*. All four regions were sampled each year. We selected only stations that occurred in embayments or lagoons for regional comparisons, which allowed comparisons of similar habitats.

Twenty-eight taxa were considered numerical dominants in this study (i.e., mean density ≥ 22 individuals m^{-2}). Densities were mean numbers of individuals (m^{-2}) among all stations sampled.

Differences in macrobenthic trophic structure were evaluated using a log-likelihood ratio or G-test (alpha = 0.05) employing intrinsic hypotheses (Zar 1984). Null hypotheses tested whether trophic group frequency distribution (trophic structure) was independent of sampling year and region. Distributions within six feeding groups were compared between two years and among four regions (i.e., 2 x 6 and 4 x 6 contingency tables). These analyses were completed using the relative abundance of each trophic group weighted for (multiplied by) the number of stations represented. The calculated test statistic was compared to the chi-square distribution, using (r-1) (c-1) degrees of freedom (d.f. = 5 for between years, and 15 for among regions). Finally, in addition to comparisons of trophic structure (G-tests), comparisons of mean total macrobenthic density (m^{-2}) among regions were made using Wilcoxon paired T-tests (alpha = 0.05) based on the ten most abundant taxa in each region.

RESULTS

Approximately 70,890 macrobenthic organisms (840 taxa; mean density, 2846.4 organisms m^{-2}) from 201 stations (603 samples) were collected. These stations were numerically dominated by *Mediomastus californiensis* (subsurface-deposit feeding polychaete; mean density, 386 m^{-2}), *Corophium cf. lacustre* (surface-deposit feeding amphipod; mean density, 178 m^{-2}), *Mulinia lateralis* (filter-feeding bivalve; mean density, 129 m^{-2}), juvenile and unidentifiable tubificid oligochaetes (subsurface-deposit feeders; mean density, 110 m^{-2}), *Probythinella louisianae* (surface-deposit feeding gastropod; mean density, 109 m^{-2}), *Streblospio benedicti* (surface-deposit/filter-feeding polychaete; mean density, 85 m^{-2}), and *Texadina sphinctostoma* (surface-deposit feeding gastropod; mean density, 79 m^{-2}) (Table 1).

Nearly equal proportions (25 - 30%) of the three categories of detritivores (FF, SDF, and SSDF) accounted for approximately 85% of the macrobenthic fauna in northern Gulf of Mexico estuaries (Table 2). Carnivores (CARN), especially nemerteans, represented approximately 12% of total macrobenthic abundance, while omnivores (OMNI) and others (XXX) each accounted for less than 4% of total macrobenthic abundance. Results from G-tests indicated that trophic distributions were not different between 1991 and 1992 (G = 4.1, critical value = 11.070; do not reject H$_0$), despite apparent shifts in the relative abundance of SSDF and FF (Table 2).

Significant differences in macrobenthic trophic structure were not found among large estuaries from the four geopolitical regions (G = 9.4, critical value = 24.996; do not reject H$_0$), despite relatively greater numbers of CARN in Louisiana and Florida, and fewer SDF in Louisiana (Table 3). Greater proportional representation by

TABLE 1

Numerically dominant macrobenthic taxa collected in Gulf of Mexico estuaries (1991-1992). Data for 201 randomly selected stations (603 samples).

Taxa	Trophic Group	Mean Density (m^{-2})
Mediomastus californiensis	SSDF	386
Corophium cf. lacustre	SDF	178
Mulinia lateralis	FF	129
unidentified Tubificidae	SSDF	110
Probythinella louisianae	SDF	109
Streblospio benedicti	SDF/FF	85
Texadina sphinctostoma	SDF	79
Paraprionospio pinnata	SDF/FF	58
Spiochaetopterus costarum	FF	54
Caecum johnsoni	OMNI	47
Myriochele oculata	SSDF	41
Hobsonia florida	SDF	40
unidentified Nemertea	CARN	36
Crassinella lunulata	FF	35
Nemertea sp. B	CARN	35
Rangia cuneata	FF	35
Nemertea sp. A	CARN	34
Tubificoides heterochaetus	SSDF	33
Parandalia sp. A	CARN	32
Ampelisca abdita	FF	27
Notomastus latericeus	SSDF	26
Magelona sp. H	SDF	26
Acteocina canaliculata	CARN	24
Balanus sp.	FF	24
Prionospio pygmaea	SDF/FF	24
unidentified Maldanidae	SSDF	23
Prionospio perkinsi	SDF/FF	23
Phoronis muelleri	FF	23
Petricola pholadiformis	FF	22

TABLE 2

Macrobenthic community trophic structure by year for northern Gulf of Mexico estuaries. Data collected from 201 randomly selected stations (603 samples).

Trophic Group	Mean number of organisms m^{-2} (proportions of each group)					
	1991 & 1992		1991		1992	
SDF	833.2	(29.3)	724.8	(29.7)	943.3	(28.9)
SSDF	782.5	(27.5)	532.5	(21.9)	1035.0	(31.7)
FF	712.7	(25.0)	737.7	(30.3)	687.9	(21.1)
CARN	349.9	(12.3)	278.3	(11.4)	422.8	(13.0)
OMNI	63.2	(2.2)	77.4	(3.2)	48.8	(1.5)
OTHER	104.9	(3.7)	86.2	(3.5)	123.8	(3.8)
TOTALS	2846.4	(100)	2436.5	(100)	3261.6	(100)

CARN in Louisiana estuaries was primarily due to high abundance of *Acteocina canaliculata* (Gastropoda), nemerteans, and *Glycinde solitaria* (Polychaeta). Stations in large estuaries of Florida also contained a higher proportion of CARN, including *Acteocina canaliculata*, nemerteans, and the carnivorous polychaetes *Lumbrineris* sp., *Goniadides carolinae*, and *Polygordius* sp. While macrobenthic trophic structure was found to be relatively similar among large estuaries from the four regions, results from Wilcoxon paired T-tests indicated that mean total macrobenthic density differed among regions ($P < 0.003$). Macrobenthos more densely populated estuaries of Mississippi-Alabama (mean density, 3160.5 m^{-2}) than estuaries of Texas (mean density, 1990.5 m^{-2}), Louisiana (mean density, 1994.8 m^{-2}), or Florida (mean density, 2441.2 m^{-2}).

DISCUSSION

Benthic macroinvertebrate communities are important functional components of estuarine ecosystems. Macrobenthic organisms alter physical and chemical conditions at the sediment-water interface, promote the decomposition of organic matter, recycle nutrients for photosynthesis, and transfer energy to other food-web components (e.g., Rhoads 1974; Boesch et al. 1976; Diaz and Schaffner 1990; Day et al. 1989). Our use of functional trophic groups to characterize the role of macrobenthos in estuaries incorporates estimates of macrobenthic community structure, and assesses or infers community function. This approach is essential to understanding estuarine ecosystems, because

it provides information about food-resource availability and food-web interactions, and may be useful for assessing differences in ecosystem structure and function over space and time.

We hypothesize that changes in proportions of trophic groups among estuaries are reflective of food allocations. For instance, estuarine habitats with an abundance of suspended food might be expected to be dominated by suspension feeders, but only when the food is limiting and/or it is ingested before reaching the bottom (Gaston and Nasci 1988). Once at the sediment surface it may be consumed by SDF, or if it is in abundance and sedimentation rates exceed consumption rates, it may be buried and consumed by SSDF. Certainly the distribution and structure of benthic macroinvertebrate communities in estuaries is governed by many interacting environmental parameters and anthropogenic factors. Species richness and abundance have been shown to vary along a number of environmental gradients including salinity (e.g., Sanders et al. 1965; Boesch 1971; Boesch 1977; Flint and Kalke 1985; Gaston and Nasci 1988), substrate or sediment type (e.g., Boesch 1973; Flint and Kalke 1985; Llanso 1985; Diaz and Schaffner 1990), and dissolved oxygen concentration (Boesch and Rosenberg 1981; Gaston 1985; Rabalais and Harper 1992). Many contaminants partition to sediments, creating a major sink and potential source for organism exposure that affect benthic distributions. For example, Gaston and Young (1992) found that sediment contaminants altered the macrobenthic trophic structure of estuaries in Louisiana.

TABLE 3

Macrobenthic community trophic structure by region for northern Gulf of Mexico estuaries (1991-1992). Data collected from 86 stations (258 samples) in selected large estuaries from four geopolitical regions.

Trophic Group	Mean number of organisms m^{-2} (proportions of each group)							
	TX (16)		LA (13)		MS-AL (44)		FL (13)	
SDF	408.1	(20.5)	258.9	(13.0)	1103.9	(34.9)	597.9	(24.5)
SSDF	584.1	(29.4)	402.3	(20.2)	682.5	(21.6)	446.4	(18.3)
FF	646.7	(32.5)	723.3	(36.2)	643.5	(20.3)	430.2	(17.6)
CARN	229.5	(11.5)	578.6	(29.0)	457.2	(14.5)	603.5	(24.7)
OMNI	56.0	(2.8)	8.1	(0.4)	163.3	(5.2)	31.7	(1.3)
OTHER	66.1	(3.3)	23.6	(1.2)	110.1	(3.5)	331.5	(13.6)
TOTALS	1990.5	(100)	1994.8	(100)	3160.5	(100)	2441.2	(100)

The numerical dominance by detritivores (85% of macrobenthic fauna) in this study is indicative of the major role of detritus in northern Gulf of Mexico estuaries. Quantities of detritus are provided to estuaries from several sources, most notably vascular plant and planktonic production (reviewed by Day et al. 1989). The fate and trophic significance of organic detritus to estuaries has been discussed in detail elsewhere (e.g., Darnell 1967; Heard 1982; Day et al. 1989; D'Avanzo and Valiela 1990; Schwinghamer et al. 1991; Kristensen et al. 1992) and will not be reviewed here, except to emphasize the salient points of this study. Understanding densities of macrobenthic organisms supported by the detrital food chain in the study area should facilitate future development of estuarine food webs and energy-flow models, and provide a more accurate assessment of the functional roles of macrobenthos in processing detritus.

The detritivores that numerically dominated estuaries of the northern Gulf of Mexico included few deep-burrowing forms that typify some large estuaries of the United States east coast (Diaz and Schaffner 1990). The SSDF were dominated by *Mediomastus californiensis*, a species of polychaete that inhabits shallow tubes. *M. californiensis* was abundant throughout the study area. There also were dense populations of FF species that inhabited the sediment-water interface, such as bivalves (especially *Mulinia lateralis*). The SDF included a greater diversity of species than the SSDF or FF. Gastropods *Probythinella louisianae* and *Texadina sphinctostoma* and several species of tube-dwelling spionid polychaetes densely populated many estuaries of Louisiana and Texas.

There have been few studies of the macrobenthic trophic structure of Gulf of Mexico estuaries. The numerical dominance by detritivores in this study generally is similar to results from Calcasieu Estuary, Louisiana (>90% detritivores; Gaston and Nasci 1988; Gaston et al. 1988), Corpus Christi Bay, Texas (generally >90%; Flint and Kalke 1985, 1986a, 1986b), and low-salinity nearshore waters off Cameron, Louisiana (an offshore extension of the Calcasieu Estuary; Gaston 1985; Gaston et al. 1985; Gaston and Edds 1994). We found higher proportions of CARN in the present characterization of all northern Gulf of Mexico estuaries than were reported for either Calcasieu Estuary or Corpus Christi Bay, perhaps reflective of the fine sediments in the latter two estuaries. Generally, greater proportions of CARN occur in sandy habitats. The ratio of carnivorous macrobenthos (i.e., infaunal predators) may be as high as 0.25 in sand or as low as 0.12 in mud (Ambrose 1984), but may vary widely depending on the predatory species that dominate each habitat. Furthermore, standing crops of CARN may vary as a function of production rates of primary consumers.

Thus, even though the ratios of trophic groups may be similar among regions, species that play those roles, and their functional behavior may vary. For instance, several species of nemerteans (CARN) and the polychaete *Sigambra tentaculata* (CARN) dominated most fine-sediment habitats in Louisiana, goniadid polychaetes such as *Glycinde solitaria* (CARN) dominated sandy mud throughout the study area, and a variety of predatory macrobenthos, especially the annelid *Polygordius* spp. (CARN), dominated sandy habitats in Florida and Texas. Each of those species plays a particular role as a CARN in the macrobenthic community, almost certainly selects and ingests specific foods, and attains its food in a unique manner. The value of using trophic groups to study macrobenthos is that trophic analyses allow characterization of a habitat by inclusion of all taxa, and results in establishment of a broad-scale model of macrobenthic resource allocation. However, the inferences that can be drawn from such a study are only as strong as the information on those species that compose each trophic group. Particular functions, population variations, and feeding of species in each region must now be analyzed before details on energy transfer at smaller scales can be interpreted. Such studies will allow researchers to establish the source and fate of energy resources of a given estuary to help interpret and test our functional model. Data of this study demonstrated the general distributions and densities of each trophic group, assessed the unique trophic characteristics of estuarine regions, and gave insight into the numerically dominant species involved.

One of the major advantages of the probability-based sampling design used for this study was the application of the data to broad-scale characterizations of estuaries in the Gulf of Mexico. These characterizations can be used to assess the condition of estuarine resources in the study area (Summers et al. 1992) and provide testable hypotheses concerning many aspects of estuarine function. This study provided a baseline for future examination of specific relationships between macrobenthic trophic structure and environmental or contaminant variables of Gulf of Mexico estuaries (see Engle et al. 1994; Brown et al. Ms.).

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THE DISTRIBUTION AND ABUNDANCE OF THE BAY ANCHOVY, *ANCHOA MITCHILLI*, IN A SOUTHEAST TEXAS MARSH LAKE SYSTEM

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ABSTRACT A one-year distribution and abundance study on the bay anchovy, *Anchoa mitchilli*, was conducted in a southeast Texas marsh-lake system from March 1990 through February 1991. Day and night collections were conducted in backwaters, lake shores, and lake centers by seining and trawling. Bay anchovies were the second most abundant fish species collected, and exhibited seasonal, diel and habitat variations in abundance and distribution. Across the study area, seasonal abundance peaks occurred in May and August following migration into the marsh and seasonal recruitment. However, within each habitat type, peaks of abundance varied in time of occurrence. Within habitats, significant differences in the mean number of anchovies occurred such that backwaters in the daytime had the greatest number followed by backwaters at night, lake shores in the daytime, and lake shores at night. Lake center collections showed no significant diel pattern. The presence of vegetation was associated with reduced anchovy numbers; however, when present, anchovies were significantly more abundant in the daytime than at night.

INTRODUCTION

Anchoa mitchilli (Valenciennes) is the most abundant species of fish in the estuarine waters of the northern Gulf of Mexico (Robinette 1983) and comprises the greatest biomass in estuaries along the Atlantic and Gulf coast states (Christmas and Waller 1973; Perret 1971; Gunter 1963). However, most of what is known about the distribution and abundance of *Anchoa mitchilli* is from off shore, near shore and estuarine studies, with little attention to marshland habitats.

Monaco et al. (1989), Robinette (1983), and Morton (1989) have summarized information on the distribution and abundance of *A. mitchilli* within large estuaries. Abundance is seasonal, and in the Gulf of Mexico varies from Spring through early winter (Robinette 1983; Ross et al. 1987; Modde and Ross 1983). In East Galveston Bay, peak abundance occurs from April to June (Arnold et al. 1960) with Galveston Bay showing an abundance of adults and juveniles from May to November (Monaco et al. 1989). In Sabine Lake, adult and juvenile *A. mitchilli* are found from March through October, with juveniles present into November (Monaco et al. 1989).

The abundance and distribution patterns of *A. mitchilli* result in part from fall and spring migrations to and from deeper waters in bays and on the continental shelf (Christmas and Waller 1973; Hildebrand 1963; Swingle and Bland 1974; Vouglitois 1987). Migration of anchovies in and out of the marsh system west of Sabine Lake is well documented (Hartman et al. 1987; Stelly 1980).

Their great abundance and small size make anchovies a key element in estuarine food webs (Hildebrand 1963; Christmas and Waller 1973; Darnell 1961; Robinette 1983). Bay anchovies are selective planktivores which link the zooplankton community with larger predatory species (Johnson et al. 1990). From spring through fall, the bay anchovy provides more than half the energy intake of predatory fish in Chesapeake Bay (Baird and Ulanowicz 1989, as cited by Houde and Zastrow 1991).

Because of their great abundance and key position in food webs, additional information on the distribution and abundance of *A. mitchilli* is needed to better understand their significance in estuarine systems. This is especially true for the associated marshes and lakes where little information exists on their distribution and abundance. This study presents information on the distribution and abundance of *A. mitchilli* in the marsh-lake system lying west of Sabine Lake in Southeast Texas. Specifically, this study examines the temporal and spatial distribution and abundance of the bay anchovy by studying three habitat types common in marshes.

METHODS

Study Area

The study area was located in southern Jefferson County, Texas, west of the south end of Sabine Lake and included Keith Lake, Sea Rim State Park, and the McFaddin

National Wildlife Refuge (Figure 1). The brackish marsh-lake system consists of nine lakes and backwaters connected by meandering streams and man-made cuts. Three habitat types that could be adequately sampled were identified. The habitat types were backwaters, lake shores and lake centers. Backwater habitats were connected to tidal creeks or lakes by restricted openings or were sheltered from the main body of a lake by a small peninsula of land or an island which lay close to shore. A key point was that backwaters were protected in some way from the wave action which occurred on the more open lakes. Lake shores lay along the edges of lakes, and lake centers were at least 100 m or more from shore. Backwater stations were the shallowest ($\bar{x}$=48.73 cm, S.D.=15.79), followed by lake shore stations ($\bar{x}$=58.1 cm, S.D.=16.1), and lake center stations ($\bar{x}$=124.9 cm, S.D.=26.5).

Stations exhibited wide variations in substrate composition. Backwater stations had the greatest amount of variation in substrate composition, which included mud, silt, and detritus in various combinations. Wave action along lake shore stations prevented silt deposition, resulting in a band of firmly compacted clay 1 to 5 m wide extending out from the shore. Beyond this band, the sediment consisted of a soft silt 6 to 30 cm deep.

Starting in May and extending to October, the aquatic plant *Ruppia maritima* covered 50% or more of stations 4 and 6, and occurred sparsely in stations 3, 5 and 10. By June, *R. maritima* occupied the entire water column of stations 4 and 6 and covered nearly 100% of both stations as well as the surrounding area. The primary difference between stations was that station 6 was very densely covered while station 4 was less densely covered. Otherwise, the coverage
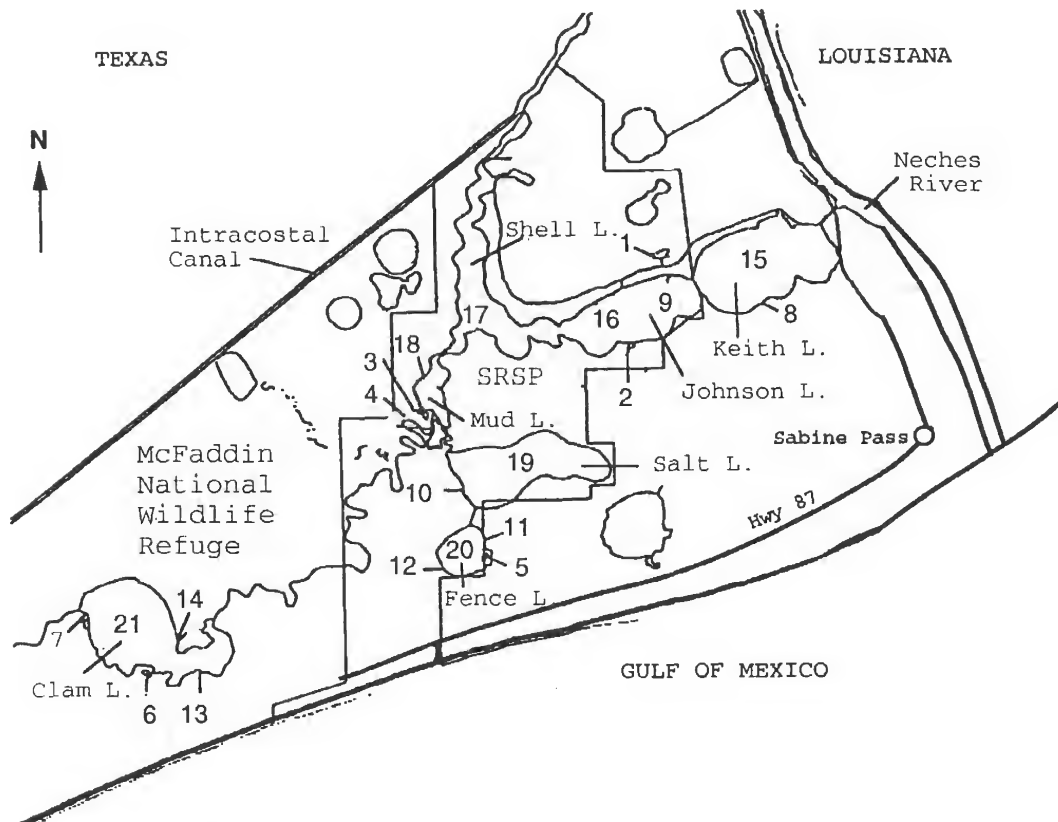

Figure 1. Study area along the Louisiana-Texas Border, Jefferson County, Texas. Incoming tides enter and leave at the east end of Keith Lake and Salt Bayou. Numbers 1-21 represent stations discussed in the text. SRSP stands for Sea Rim State Park which lies between the two sets of vertical and horizontal straight lines representing the park boundary.

was nearly uniform within the station. The *R. maritima* was replaced with filamentous algal mats in October and November. All vegetation died back by December.

Protocol

From March 1990 through February 1991, 242 collections were made in the study area. Twenty-one stations were established based on the three habitat types:

- back waters (stations 1-7)
- lake shores (stations 8-14), and
- lake centers (stations 15-21).

Stations were numbered east to west following the incoming tides. Lake shores and backwaters were marked with stakes 15 m from the bank. Lake centers were not staked. Stations were sampled monthly with night collections made every other month. Lake shores and backwaters were sampled by pulling a seine from the station markers to the bank. The seine was 6.1 m long, possessed 6.35 mm knitted mesh, and a 4.6 m opening maintained by tying a rope to the seine poles. Lake center stations were sampled with a 3.66 m trynet (25 mm stretch mesh) fitted with a 6.35 mm bar mesh cod-end liner. The trynet was pulled by boat for three minutes for a distance of approximately 430 m. This distance was originally estimated by timing how long it took to pull the net over 125 m marked off by stakes set out in a marsh lake.

All anchovies captured were hardened in 10% formalin for 24 hours, washed in water 24 hours, and preserved in 55% isopropyl alcohol. Specimens were returned to the laboratory and enumerated. Type and percent submerged vegetation within stations was visually estimated. Problems with scheduling, equipment failure, and weather caused the postponement or elimination of some collections listed in Griffith (1993).

RESULTS

During the 12-month collecting period, 49 fish and 14 invertebrate species were collected. Fish represented 67% of all specimens collected and invertebrates 33%. The four dominant taxa were *Brevoortia patronus* (24,321), *A. mitchilli* (13,266), *Menidia beryllina* (5,697), and *Micropogon undulatus* (5,183). A full breakdown of all species and their yearly totals can be found in Griffith (1993).

Bay anchovies comprised 23.3% of the total fish catch with a per catch average of 54.8 (N=242, S.D.=124.8). The temporal distribution and abundance of bay anchovies

exhibited two peaks which were seen in all three habitats (Figure 2). Generally abundance increased from March through May, decreased in June, increased in July, and peaked a second time in August. After August, abundance steadily decreased until February. In lake shore and lake center stations, the first peak abundances of anchovies occurred in April, one month earlier than the in backwaters. The second peaks of abundance occurred in November in lake shores, July in lake centers, and August in backwaters. While anchovies were present in low numbers in lake shore and lake center stations in June, they were nearly absent in backwater stations. The anchovies that were present were mostly juveniles with only a few adults present. Within each habitat type there were no significant differences in the use of stations by bay anchovies (Oneway ANOVA; Backwaters: N=81, df=80, F=1.410, P=0.221; Lake shores: N=83, df=82, F=1.490, P=0.193; Lake Centers: N=78, df=77, F=1.130, P=0.355).

Differences in the diel distribution of anchovies occurred in backwaters and lake shores. In all cases, nighttime collections had lower means than daytime collections, while backwater stations always had the highest means (Table 1). A oneway ANOVA using as treatments day and night collections from backwaters and lake shores (N=164; df=3,160; SD=144.4; F=2.990; P=0.033) followed by a Tukey test showed significant differences between day and night collections in both habitats. The Tukey test revealed that each treatment value calculated (backwaters day-backwaters night = 59.50, backwaters night-lake shores day = 21.10, lake shores day-lake shores night = 4.69) exceeded the critical value (3.68), indicating significant differences in densities within each habitat for day and night collections. The relative abundance of anchovies/habitat/photoperiod was: backwater stations, daytime ($\bar{x}$=129.6) > backwater stations, night ($\bar{x}$=70.1) > shoreline stations, daytime ($\bar{x}$=49.0) > shoreline stations, night ($\bar{x}$=44.3). Lake center collections were not significantly different between day and night collections (N=78, day $\bar{x}$=21.68, night $\bar{x}$=12.00, df=51, t=1.570, P=0.120).

The presence of dense stands of *R. maritima* and filamentous algae from May-October in backwater stations 4 and 6 allowed two analyses to be made. The first analysis permitted the comparison of vegetated against unvegetated areas. This was done by comparing stations 4 and 6 to stations 1, 3 and 5 for the time period when vegetation was present. Stations 1, 3, and 5 were used as controls because their physicochemical structure was most like stations 4 and 6 (Griffith 1993). The analysis showed that heavily vegetated backwaters possessed significantly fewer anchovies ($\bar{x}$=54.0) per collection than unvegetated backwaters ($\bar{x}$=161.0) (N=59, DF=53, t=-2.210, P=0.032).
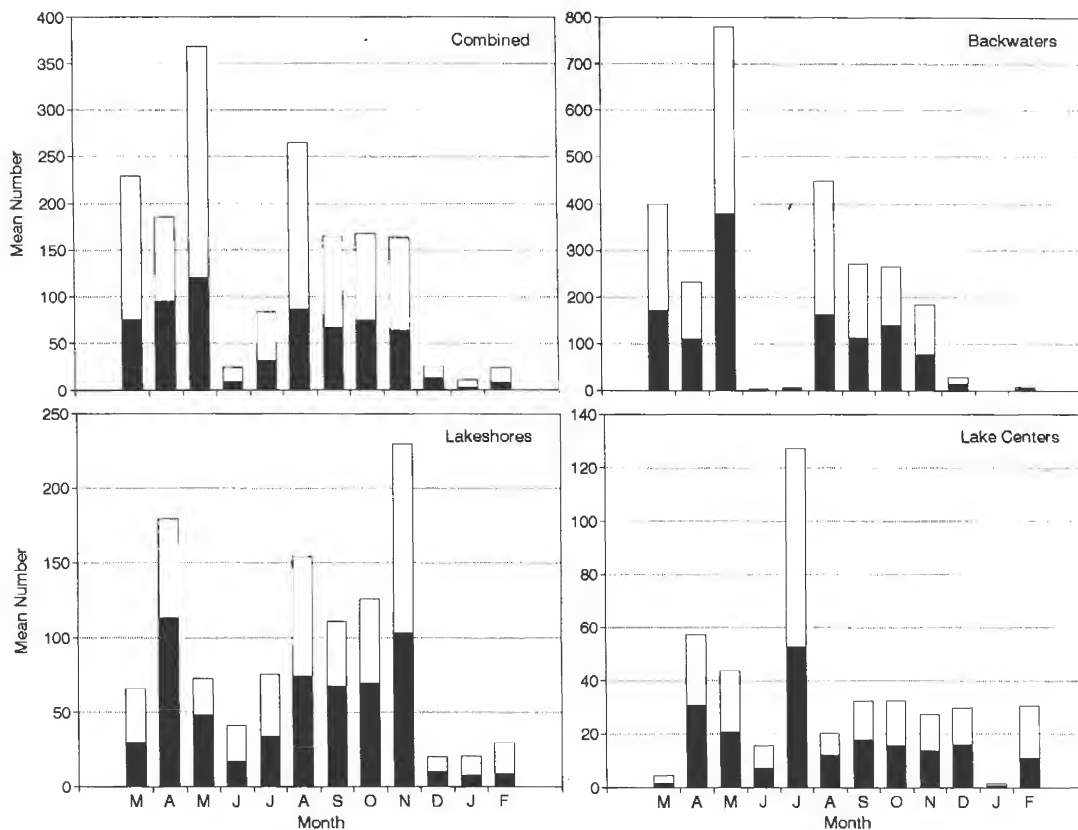
Figure 2. Mean number of anchovies collected per month in each habitat type and all habitat types combined. Solid bars represent the mean number of anchovies per month. Open bars represent the standard deviations.

TABLE 1

Yearly mean catch of *A. mitchilli* by habitat and time period (Day=L and Night=D), March 1990-February 1991.

Habitat	L/D Cycle	N	Mean	STDEV.	Min.	Max.
Backwaters	Day	40	129.6	235.8	0	1101
	Night	41	70.1	146.5	0	810
	24 hrs.	81	99.5	196.8	0	1101
Lake shores	Day	41	49.0	65.3	0	329
	Night	42	44.3	58.4	0	234
	24 hrs.	83	46.6	61.5	0	329
Lake Centers	Day	41	21.7	36.8	0	163
	Night	37	12.0	13.4	0	50
	24 hrs.	78	17.1	28.5	0	163
Combined	24 hrs.	242	54.8	124.8	0	1101

The second analysis compared vegetated areas at night against vegetated areas in the daytime. Because of skewedness, a Mann Whitney U-test was used to test the rank order of the data (Sokal and Rohlf 1981). The results showed that daytime collections of *A. mitchilli* (N=6, $\bar{x}$=99.0) were significantly higher than nighttime collections (N=6, $\bar{x}$=48.7,P=0.0127).

DISCUSSION

Reproduction, habitat structure, diel period, season, and vegetation were all associated with anchovy abundance and distribution. Seasonal distributions and abundances of *A. mitchilli* in the study area were controlled in part by reproductive periods and seasonal migrations to and from the marsh. Peak abundances of adults and juveniles in the study area occurred during April-May and July-August, with periods of low abundance occurring in June-July and December-February, depending on the particular habitat. The periods of high and low abundance observed in the marsh lake system are similar to those observed by Herke (1971) and most likely resulted from reproductive periods which occurred two to three months prior to the peak abundances. Manaco et al. (1989) reported spawning, eggs, and larvae were common March through November in nearby Sabine Lake. Larval growth is rapid (Cowan and Houde 1990), and larval and juvenile stages may be completed in 2.5 months with some young-of-the-year maturing by late summer, although most over winter before maturing the following year (Houde and Zastrow 1991).

Stelly (1980) found a large net movement of bay anchovies out of the study area in November and December, while a smaller net movement out was detected in May and June accounting for some of the reduced numbers found in January-February and June-July, depending on the habitat type. Along the Gulf and Atlantic coasts, the bay anchovy migrates during winter to deeper waters and out to the inner continental shelf, returning to the estuaries in spring (Christmas and Waller 1973; Hildebrand 1963; Vouglitois 1987; Swingle and Bland 1974). While all the evidence indicates that the bay anchovy is migrating in and out of the study area, at least a small percentage of anchovies remain in the marsh year round.

Habitat and diel periodicity were also associated with anchovy distribution and abundance. Anchovies were more abundant in backwaters than lake shores and were more abundant in the daytime than at night in both habitats. Day and night time concentrations of *A. mitchilli* within lake center stations were not significantly different from each other. This would suggest that any diurnal migrations from backwater and lake shore stations were not solely to lake center stations, but to other areas within the marsh not sampled in this study.

Heavily vegetated backwaters possessed significantly fewer anchovies per collection than did unvegetated backwaters, indicating vegetation was a limiting factor. Herke (1971) found a similar pattern in his work on semi-impounded vegetated areas. Cornelius (1984) found *A. mitchilli* characteristic of unvegetated mud substrate, while others have captured *A. mitchilli* over, but not in, *Thalassia* seagrass beds (Scott Holt per. comm.). Castro and Cowen (1991) found no difference in the density of day and night collections of larval *A. mitchilli* in vegetated areas, suggesting that the presence of vegetation primarily affects juveniles and adults. *Anchoa mitchilli* is an opportunistic, selective zooplanktivore (Johnson et al. 1990) that may be less successful at foraging in dense vegetation. This hypothesis is supported by the fact that anchovies collected in vegetated areas have lower body weights than those collected from unvegetated areas (Herke 1971). However, *A. mitchilli* was significantly more abundant in vegetated areas in the daytime, suggesting that it may use dense stands of unbroken vegetation as a refuge from predators (Griffith 1993) and then move out to forage at night (Johnson et al. 1990).

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A Study of Factors Influencing the Hatch Rate of *Penaeus vannamei* Eggs. I. Effects of Size, Shape and Volume of the Spawning Tank

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A STUDY OF FACTORS INFLUENCING THE
HATCH RATE OF *PENAEUS VANNAMEI* EGGS. I.
EFFECTS OF SIZE, SHAPE AND VOLUME OF THE SPAWNING TANK

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ABSTRACT The hatch rate of *Penaeus vannamei* eggs spawned by individual females in square and round tanks and in different volumes of seawater was determined. The mean hatch rates ranged from 17.3% to 64.9% and were not significantly different for volumes of 50, 100 and 200 L nor for square or round tanks of equal water volumes. Hatch rate was significantly affected by the size of the spawning tank.

INTRODUCTION

Aquaculture accounts for over 25% of the world's shrimp production (Rosenberry, 1991). The farming of shrimp requires acquisition of seed stock which is reared to marketable size. Seedstock may be harvested from the wild or produced from broodstock. Broodstock may be sourced from the wild or acquired from maturation facilities. In either case, mated oviparous shrimp are spawned under captive conditions in order to collect the larvae. A variety of systems have been used to spawn marine shrimp. Eggs or nauplii may be collected directly from the tank in which maturation and matings take place (Laubier-Bonichon and Laubier 1979; Brown et al. 1980; Lawrence et al. 1980; Simon 1982; Chen et al. 1991; Ogle 1992). However, many facilities remove the mated females to a separate tank for spawning. Wyban and Sweeney (1991) and Bray and Lawrence (1992) report the stocking of a single mated female into a tank while Lawrence et al. (1980), Kittaka (1981), Aquacop (1983), Yang (1975), Tabb et al. (1975) and Treece (1985) cite that several mated females may be placed in a common tank for spawning. In most cases, spawning and hatching are accomplished in one tank and the nauplii are collected and transferred to another tank for larval rearing. However, Salser (1978) and Bray and Lawrence (1992) recommend that after the shrimp spawn, eggs be removed to a separate tank for hatching. Tanks utilized for spawning and hatching have been as large as 145,800 L (Kittaka, 1981) and as small as 10 L (Mock and Murphy 1971). Bray and Lawrence (1992) suggest 75 L as the minimum tank size with 100 to 150 L circular tanks supplied with lids as the preferred choice for spawning and hatching. Browdy (1992) suggests using a tank size of 150-500 L and Browdy and Samocha (1985a and 1985b) report that simple flat-bottom tubs are sufficient for the spawning

and hatching of eggs. Aquacop (1983) utilizes conical bottom tanks. A comparison of the two tank types, conical and flat-bottomed, with *P. setiferus* could demonstrate no significant differences in hatch rates (Browdy, in preparation). Lotz and Ogle (1994) report an increasing hatch rate of *P. vannamei* with an increasing volume of the spawning tanks. However, the spawning tanks varied in size and shape. As these are the only comparative studies on the effect that tank shape and volume have on hatch rates, the present study was undertaken with *P. vannamei*.

MATERIAL AND METHODS

Three different tank types were used for spawning mated *P. vannamei* females. Rectangular polyethylene tubs, 0.51 m x 0.53 m x 0.32 m, with a bottom area of 0.27 m² were utilized as one of the tank types. The other two tank types were both round fiberglass tanks and are referred to as small and large. The small tanks had a diameter of 0.61 m and a depth of 0.45 m with a bottom area of 0.29 m² while the large tanks had a diameter of 1.12 m and a depth of 0.60 m with a bottom area of 0.98 m² (1 m²).

The spawning tanks were filled with a measured volume of seawater. Natural baywater pumped from Davis Bayou in the Mississippi Sound was allowed to stand for several weeks to allow suspended solids to settle. Artificial seasalt (Marine Environment, San Francisco, CA) was added to increase the ambient salinity of 25 ppt to a salinity of 30 ppt. The water was filtered through a particulate five-micron RS pleated polyester fabric media cartridge (Amtek, Flowrite, Inc., 3345 Halls Mill Rd., Mobile, AL 36606) and granular activated carbon (Amtek) before use. Sodium EDTA was added at the rate of 3 ppm.

Shrimp were matured and mated in large commercial sized maturation tanks (Ogle 1992). Mated females were sourced from the maturation tanks in the evening and placed individually into the spawning tanks. Moderate aeration was provided by a single airstone throughout spawning and hatching. The shrimp were checked for spawning after two to three hours and spent females were returned to the maturation tanks.

The number of eggs was estimated by subsampling. The water in the spawning tank was stirred and five-10 ml subsamples were collected. Subsamples were taken from the four compass directions and the center of the tank. The samples were transferred to a petri dish and the eggs counted. Data were averaged and the total number of eggs calculated. After 12-15 hours, the number of nauplii was determined in the same fashion and the hatch rate calculated (% H = # nauplii/# eggs x 100). Only spawns that hatched were analyzed. Data were compared by ANOVA and significant (alpha = 0.05) differences noted.

The large ($1m^2$) tanks were used to study the effect of water volume on hatch rate with 50, 100 or 200 L of seawater placed in a tank for each shrimp. Twelve shrimp were individually spawned in each of the three water volumes, for a total of 36 shrimp. Fifty L of seawater were used in all subsequent studies. The effect of tank shape on hatch rate was determined by comparing spawns in the square tubs, $0.27 m^2$, and the small fiberglass round tanks,

$0.29m^2$. A total of 14 individual spawns were recorded for the square tanks and 15 individual spawns were recorded for the small round tanks. An additional 14 animals spawning in the small round fiberglass tanks were compared to 14 animals which spawned in the large round fiberglass tanks to determine the effect of tank size on hatch rate. In all studies, eggs were left in the spawning tanks until hatching occurred. After the eggs hatched, the tanks were drained, cleaned and filled with new seawater.

RESULTS

There were no significant differences for the effect of the water volume in the spawning tanks or the shape of the spawning tanks on hatch rates of *P. vannamei* eggs (Table 1). The average hatch rates for eggs spawned in 50, 100 and 200 L of water were 45.2, 55.2, and 42.4%, respectively. The average hatch rates for eggs spawned in the square and the small round tanks were 25.4 and 18.2%, respectively.

There was a significant effect of tank size on the hatch rates. The hatch rates for eggs spawned into a tank of $0.29 m^2$ and $1 m^2$ were 17.3% and 64.9%, respectively.

Overall, the minimum spawn size was 39,000 eggs and the maximum spawn size was 230,000 eggs. The minimum egg density was 780/L and the maximum was 4,600 eggs/L. This is equivalent to 10,000 to 900,000 eggs/m^2.

TABLE 1

The effect of tank volume, shape and size on the hatch rate of *Penaeus vannamei* eggs.

| Study | Treatment | Replicates N | Hatch Rate | | | Significance |
			Mean %	Range %	S.E.	
Volume	50 L	12	45.2	3.8 - 89.3	7.10	NS
	100 L	12	55.2	15.2 - 100.0	7.21	NS
	200 L	12	42.4	1.5 - 90.0	8.54	NS
Shape	Square	14	25.4	3.8 - 57.8	4.15	NS
	Round	15	18.2	2.4 - 51.3	5.26	NS
Size	$0.29 m^2$	14	17.3	2.0 - 51.3	4.15	SIG
	$1.00 m^2$	14	64.9	15.2 - 100.0	6.69	SIG

Volume - $1 m^2$ round fiberglass tank. Shape - square, $0.27 m^2$ polyethylene tanks with 50 L of water; round, $0.29 m^2$ fiberglass tanks with 50 L of water. Size - round tanks with 50 L of water. SIG = significant. NS = non-significant.

DISCUSSION

While there was a significant effect of the tank size on the hatch rate of *P. vannamei* eggs, the reason is unclear. The volume in both the large and small tanks was 50 L which created a greater water depth in the smaller tank. The difference in depth does not appear to have an effect on hatching as demonstrated in the experiment on water volumes in this study. This suggests that as long as the female is allowed a sufficient area for unrestricted spawning, the depth of the water beneath the shrimp appears to have no effect on hatch rate. Instead, tank area may play an important role in hatch rate. The average hatch rate reported for *P. vannamei* of 30% to 47% (Wyban and Sweeney 1991) is consistent with the rates reported here of 17.3% to 64.9%.

It should be pointed out that the hatch rates reported here include three discrete events: spawning, fertilization and hatching. Spawning of *P. vannamei* occurs as the female slowly swims in circles near the surface of the water. It is possible that restricting the movement of the shrimp to a smaller area may interfere with fertilization of the eggs which would result in a lower hatch rate. It is also possible that the hatch rate may be directly influenced by the bottom area of the tank.

As the mechanisms involved in egg fertilization are not known, it is unclear how restricting the swimming activity of the shrimp during spawning would influence fertilization and hatch rates. Heldt (1938) and Hudinaga (1942) have suggested that sperm released from the spermatophore are trapped by the ventral setae of the third and fourth pereopods which come into contact with the eggs as they are released. We have been unable to detect sperm on the pleopods or pereopods of mated *P. vannamei* by microscopic examination. Fertile spawns frequently result from matings for which the spermatophore is missing. Fertile spawns have also resulted from females which do not swim but lie perfectly still during spawning. In such incidence, the hatch rate is extremely low (Ogle 1993b).

The effect of egg density on hatching is also unknown. Primavera (1980) has recommended that the egg density in spawning tanks for *P. monodon* not exceed 2,500 to 3,000 eggs per liter. In another study, Primavera *et al.* (1977) found no effect on the hatching of *P. monodon* eggs at densities of 7000/l. However, they did not report the results in terms of area (eggs/m^2). *P. monodon* eggs are larger than *P. vannamei* eggs (Ogle, in preparation) so the densities used here of 780 - 4,600 eggs/L should have no effect on the results. This is also supported by the fact that the volume of water did not significantly affect the hatch rate. Further research could be directed to determined the effect of tank area on fertilization rates and hatch rates.

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A Study of Factors Influencing the Hatch Rate of *Penaeus vannamei* Eggs. II. Presence of a Spermatophore

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A STUDY OF FACTORS INFLUENCING THE HATCH RATE OF *PENAEUS VANNAMEI* EGGS. II. PRESENCE OF A SPERMATOPHORE

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ABSTRACT Eighty-three mated *Penaeus vannamei* females were sourced from a commercial sized maturation tank. The hatch rate was recorded for those shrimp based on the presence of a full spermatophore, a partial spermatophore or the loss of the spermatophore during sourcing and handling. The hatch rates were not significantly different among females for the three spermatophore conditions. The mean hatch rates were 48.8% for full spermatophores, 43.1% for partial spermatophores and 55.6% for lost spermatophores. The location of the sperm at fertilization and the precise mechanisms of fertilization are still unknown.

INTRODUCTION

Reproduction of open thelycum penaeid (Litopenaeidae) shrimp has been discussed by Chamberlain (1985), Dall et al. (1990), Bray and Lawrence (1992), and Browdy (1992). Ovarian maturation in open thelycum penaeid shrimp occurs during the intermolt cycle of the adult female. Mating takes place soon after dusk, four to five hours prior to spawning. Mating is accomplished with the males's transference of a compound spermatophore to the female's thelycum. Apparently, fertilization of the eggs occurs simultaneously with spawning.

Early researchers working with *P. setiferus* were rarely able to collect females with attached spermatophores (Andrews 1911; Burkenroad 1934; Heegaard 1953). Early reports noted that the spermatophores of *P. setiferus* are easily dislodged (Weymouth et al. 1933; King 1948; Cook and Murphy 1966; Perez-Farfante 1969, 1975). In fact, Weymouth et al. (1933) reported that out of 18,487 females examined, spermatophores were found on only 20 of the animals. Cook (1967) obtained fertilized eggs from female *P. setiferus* bearing no spermatophores. While examining wild female *P. setiferus* in which no spermatophores were found attached, Bray et al. (1983) detected minute sperm masses 2 mm in diameter. These sperm masses cannot be seen unless the third pair of walking legs are folded back and the thelycum closely examined. Of 103 mated animals examined from the wild, they noted the condition of a "sperm mass only" to be most prevalent (54%), as opposed to partial spermatophores (19%) and full spermatophores (27%). They also noted the sperm mass only condition for *P. setiferus* held in tanks. There was no significant difference in the number of nauplii or the hatch rate for the three spermatophore conditions.

Bueno (1990), working in tanks with another open thelycum Litopenaeid, *P. schmitti*, noted 79% of the females with full spermatophores and 21% of the mated females with sperm mass only. He found no significant effect when correlating the spermatophore condition with fertilization and hatch rate.

During the captive reproduction of *P. vannamei*, mature mated females are removed from the large maturation tanks and placed in small spawning tanks. The females are selected based on the presence of either a full or partial spermatophore. It is also common for the full spermatophores of *P. vannamei* to become dislodged and lost during handling. In an attempt to document the effect of the spermatophore condition on hatch rates for *P. vannamei*, the following data are presented.

MATERIALS AND METHODS

The shrimp, *P. vannamei*, were matured and mated in large commercial sized maturation tanks (Ogle 1992). Mated females were sourced for mating and removed from the maturation tanks in the evening. Mated females were placed, one per tank, into 1m² round fiberglass spawning tanks containing 100 L of seawater (Ogle 1995). Prior to sourcing, the spawning tanks were filled with filtered baywater which had been adjusted from 25 ppt to 30 ppt salinity by the addition of an artificial seasalt (Marine Environment, San Francisco, CA). Moderate aeration was provided by a single airstone. The shrimp were checked for spawning after two to three hours and spent females were returned to the maturation tank.

The number of eggs was estimated by subsampling. The water in the spawning tanks was stirred and five 10 ml

subsamples were collected from the four compass directions and from the tank center. The samples were transferred to a petri dish and the eggs counted. Data were averaged and the total number of eggs calculated. After 12-15 hours, the number of nauplii was determined in the same fashion and the hatch rate calculated.

A total of 83 mated females was sourced from the maturation tanks. Condition of the spermatophore (full, partial or lost during sourcing) was noted. The effect of the three spermatophore conditions on the hatch rates of all spawns was compared by AVOVA where alpha < 0.05 was significant. In some of the individual spawns, none of the eggs hatched. The spawns which produced no nauplii (no hatch) were eliminated from the data set and the data reanalyzed.

RESULTS

The hatch rate of *P. vannamei* eggs was not significantly influenced by the loss or partial presence of the spermatophore (Table 1). The hatch rate for 49 shrimp retaining a full spermatophore was 31.8% (S.E. 4.68). The hatch rate for the 16 shrimp retaining only a partial spermatophore was 24.2% (S.E. 7.52). The hatch rate for the 18 shrimp which lost their spermatophores was 18.2% (S.E. 5.56). These differences were not significant given the large range in hatch rates (0-100%) and correspondingly large standard error.

When the spawns which did not hatch were eliminated from the data set, there was still no significant effect of the spermatophore condition on hatch rate. The hatch rate for 32 shrimp with a full spermatophore was 48.8% (S.E. 5.03). The hatch rate for nine shrimp with a partial spermatophore was 43.1% (S.E. 9.33). The hatch rate for ten shrimp with no spermatophore was 32.7% (S.E. 7.24). These differences are not significant given the range in hatch rates (3.8-100%) and correspondingly large standard error.

DISCUSSION

There is no significant effect of the spermatophore presence at the time of spawning on hatch rate of *P. vannamei*. This was the conclusion reached by Bray et al. (1983) for *P. setiferus*. The 13 shrimp with full spermatophores produced 53,000 (S.E.M. ± 24,700) nauplii for a hatch rate of 26.2% (S.E.M. ± 9.13). The 11 animals with wings only produced 109,000 (S.E.M. ± 38,400) nauplii for a hatch rate of 37.2% (S.E.M. ± 8.79). The 52 animals retaining a sperm mass only produced 92,000 (S.E.M. ± 13,800) nauplii for a hatch rate of 35.2% (S.E.M. ± 3.84).

Bueno (1990), working with *P. schmitti*, could find no significant effect on either hatch rate or fertilization rate due to the condition of the spermatophore. He reported that 408 shrimp with full spermatophores produced an average of 76,558 nauplii (s.d. ± 42,694) per shrimp and 110 shrimp with a partial spermatophore produced an average of 89,903 (s.d. ± 54,386) nauplii per shrimp. In addition, he also examined the eggs and calculated a percent

TABLE 1

Hatch rate of *Penaeus vannamei* in relation to spermatophore condition.

	Full	Partial	Lost
All spawns			
% hatch	31.8	24.2	18.2
n	49	16	18
max	100.0	100.0	63.4
min	0.0	0.0	0.0
SE	4.68	7.52	5.56
Spawns that hatched			
% hatch	48.8	43.1	32.7
n	32	9	10
max	100.0	100.0	63.4
min	3.8	8.0	6.4
SE	5.03	9.33	7.24

fertilization. Not all fertilized eggs hatch. For the shrimp with full spermatophores, the percent fertilization was 73.46 (s.d. ± 28.03). For the shrimp with a partial spermatophore, the percent fertilization was 71.50 (s.d. ± 30.78). Despite the large sample size, significant differences could not be determined due to the large variations that exist in fertilization and hatch rates for marine shrimp.

Weymouth et al. (1933) reasoned that since the spermatophores are easily dislodged from the females, the eggs must be spawned and fertilized before the spermatophores are lost. Although we now know this is not the case, the actual mechanisms behind egg fertilization in Litopenaeid shrimp is still unclear.

Mated females are sourced out of maturation tanks 1-2 hours after mating has taken place. It has been suggested that the spermatophore ruptures (Perez-Farfante 1975; Bente 1977) and that sperm present on the pereiopods of the female (Heldt 1938; Hudinaga 1942) fertilize the eggs as they brush past. To date, efforts at this laboratory to microscopically verify the presence of sperm on the pleopods and pereiopods of spawning *P. vannamei* have been unsuccessful. The artificial placement of a sperm mass at several locations on mature *P. setiferus* did not significantly affect the hatch rates (Bray et al. 1983), although the hatch rate of the artificially inseminated shrimp was significantly less than that of naturally mated shrimp.

It is not known how sperm are released from the spermatophore. Spermatophores placed in test tubes of seawater at this laboratory did not rupture or release sperm even after five hours exposure. In some cases when *P. vannamei* are entirely quiescent during spawning, the eggs descend without coming into contact with the spermatophore, pleopods or pereiopods, but they still hatch (Ogle, personal observation). In such cases, a dense mass of eggs are deposited on the bottom of the tank and the hatch rate is extremely low.

King (1948) stated that the spermatophore opened and released sperm at the time of spawning, which in turn may be caused by a substance secreted with the expelled eggs. King felt that this substance may chemically or physically break down the spermatophore. In contrast, as verified in this report, fertilization of the eggs is accomplished even though the spermatophore is completely lost prior to spawning. Therefore, it is suggested here that the sperm or sperm mass is released from the spermatophore shortly after mating and several hours before spawning. The location of the sperm at the time of fertilization and the mechanism of egg fertilization are unclear, as is the "need" for the rather complex spermatophore. Female shrimp have been observed manipulating the spermatophore with the pereiopods after mating (Ogle, personal observation). It is not known whether this ruptures the spermatophore or possibly transfers sperm to the oviducts.

This report substantiates for *P. vannamei*, as for *P. setiferus* and *P. schmitti*, that the presence of the spermatophore at spawning does not significantly affect the hatch rate.

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Gametogenic Cycle in the Non-Native Atlantic Surf Clam, *Spisula solidissima* (Dillwyn, 1817), Cultured in the Coastal Waters of Georgia

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GAMETOGENIC CYCLE IN THE NON-NATIVE ATLANTIC SURF CLAM, *SPISULA SOLIDISSIMA* (DILLWYN, 1817), CULTURED IN THE COASTAL WATERS OF GEORGIA

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ABSTRACT This study describes the gametogenic cycle of the Atlantic surf clam, *Spisula solidissima* (Dillwyn, 1817), cultured from fall to spring in the coastal waters of Georgia, where it is non-native. Early active stages of gametogenic development began in November, with the majority (83%) of the animals in the early active stage by December. Gonadal indices increased to late active stages by March, with ripe individuals present in April. Spawning commenced in May and continued into June. Sex ratio (0.48 female to 1.00 male) was significantly unequal. Results of this study indicate that clams achieved sexual maturity and spawned when cultured in the coastal waters of Georgia. An aquacultural enterprise in Georgia could obtain broodstock for the production of the following fall's seed crop from the prior year's growout field planted clams before their spring harvest.

INTRODUCTION

The Atlantic surf clam, *Spisula solidissima* (Dillwyn, 1817), occurs from Nova Scotia to North Carolina (Abbott 1974) and represents the second most valuable clam fishery in the United States. The potential for the development of aquaculture for yearling surf clams in the northeastern US has been investigated (Goldberg 1980, 1989) and attempted commercially (Monte, personal communications). In Georgia, juvenile Atlantic surf clams planted in fall and harvested in spring exhibited some of the fastest growth rates recorded for this species. Clams planted in November (at approximately 10 mm in shell length) achieved a mean size of 50 mm in shell length by May (Goldberg and Walker 1990; Walker and Heffernan 1990a,b,c,d). The size of this animal is ideal for the raw or steamer clam markets (Krzynowek et al. 1980; Krzynowek and Wiggin 1982). Experimental growout trials in Georgia indicate that the potential for surf clam aquaculture in the southeastern U.S. is excellent (Goldberg and Walker 1990; Walker and Heffernan 1990a,b,c,d). Surf clams must be harvested by mid to late spring (April/May), since high summer water temperatures (>28°C) that occur in coastal Georgia would cause physiological stress resulting in 100% mortality (Goldberg 1989).

The Georgia Department of Natural Resources currently bans the importation of bivalve seed into the state due to the threat of possible importation of shellfish pathogens along with the seed stock. Therefore, an aquacultural industry would need another method of continuing the propagation and replenishment of stocks for the following year's crop. This study determines the gametogenic cycle of the non-native Atlantic surf clam when cultured under field conditions in the coastal waters of Georgia and investigates whether or not field-planted animals reach sexual maturity and spawn within a single year. If this occurs, then a major biological hurdle to the development of this clam as a commercial aquacultural species for the southeastern US fishermen will be overcome.

MATERIALS AND METHODS

The first generation of surf clams was spawned within the Shellfish Research Laboratory in the spring of 1991 under guidelines established for the culturing of exotic species by the International Council for the Exploration of the Seas (ICES). The second generation, used in this experiment, was spawned in the laboratory on 5 May 1992. Juveniles were cultured in upwellers and fed *Skeletonema* sp. and *Isochrysis galbana* (Tahitian strain) within a temperature controlled room [23 ± 2.0 (SE) °C] from June until 10 October 1992. On 10 October 1992, clams [19.4 ± 0.12 (SE) mm shell length] were field-planted in 12 mm mesh vinyl coated wire cages (N = 9 cages) at a density of 200 clams per cage (1 m x 1 m x 0.25 m cage). Cages were buried approximately 0.1 m deep at the mean low water mark on a sand flat near the mouth of House Creek, Little Tybee Island, Georgia (Figure 1). In mid-March, cages and animals were transplanted to the spring low water mark. This was done to extend the length of the feeding period in the hopes of enhancing growth rate.

Between October 1992 and June 1993, 30 clams were randomly collected each month from a different cage, measured for shell length (i.e. longest possible measurement,
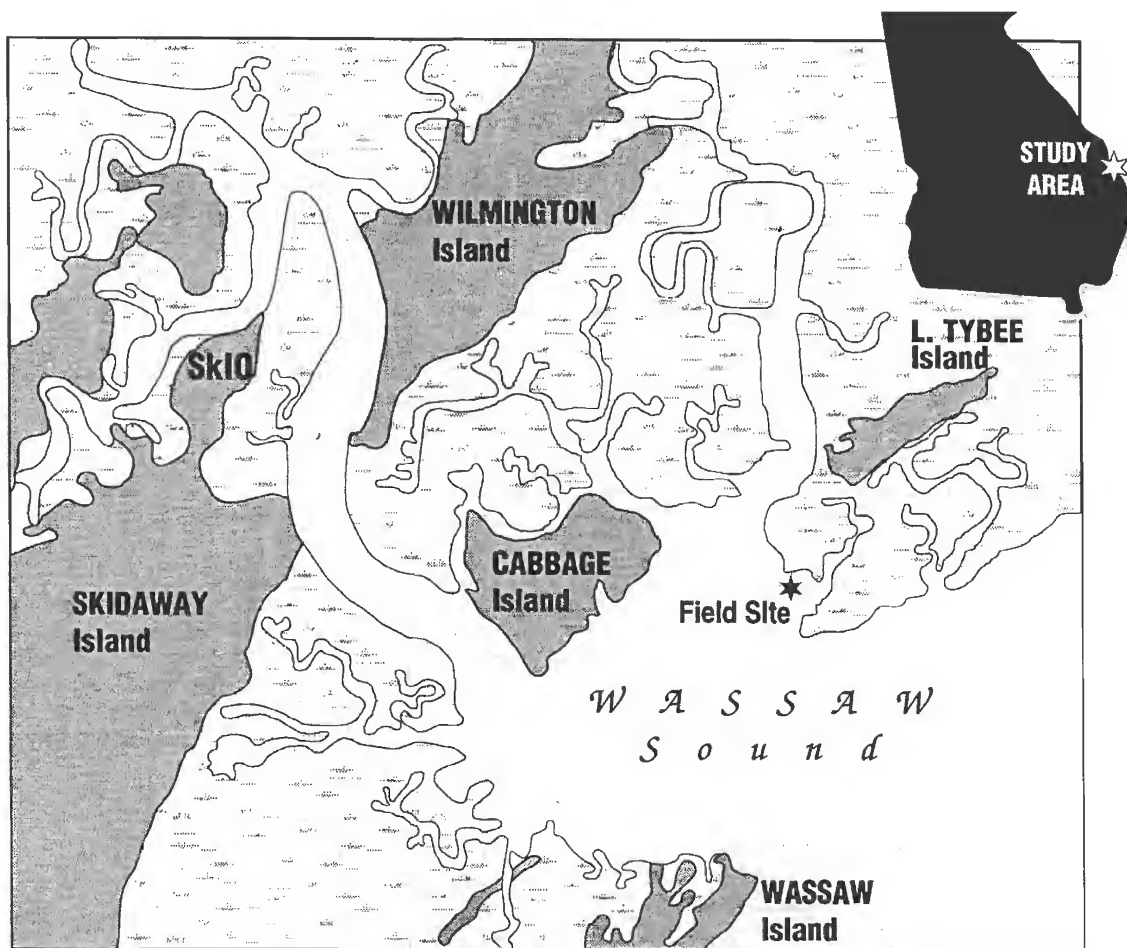
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Figure 1. Location of field growout site of *Spisula solidissima* at the mouth of House Creek, Little Tybee Island, Georgia. SkIO (Skidaway Institute of Oceanography) denotes the site where daily temperatures were recorded.

anterior-posterior), and a mid-lateral gonadal sample (ca 1 cm^2) was dissected from each clam. Gonadal tissue was fixed in Davidson's solution, refrigerated for 48 hours, washed with 50% ethanol (Etoh), and held in 70% Etoh until processing. Tissue samples were processed according to procedures outlined in Howard and Smith (1983).

Prepared gonadal slides were examined with a Zeiss Axiovert 10 microscope (20X), sexed, and assigned to a developmental stage as described by Ropes (1968) and Kanti et al. (1993). Staging criteria of 0 to 5 were employed for Early Active (EA=3), Late Active (LA=4), Ripe (R=5), Partially Spawned (PS=2), Spent (S=1), and Inactive (IA=0). Monthly gonadal index (G.I.) values were determined for

each sex by averaging the number of specimens ascribed to each category score.

Sex ratios were tested against a 1:1 ratio with Chi-Square statistics (Elliott 1977). Statistical analysis of mean gonadal index values was performed by Analysis of Variance (ANOVA) and Tukey's Studentized Range Tests (SRT) using SAS for PC software (SAS Institute 1989).

Water temperatures were recorded daily at 0800 from October 1992 to June 1993 at the dock of the Marine Extension Service, Skidaway Island, Georgia, and are presented as biweekly means in Figure 2. This site is approximately 4.5 nautical miles inland from the site where clams were field-planted. Temperature recorders
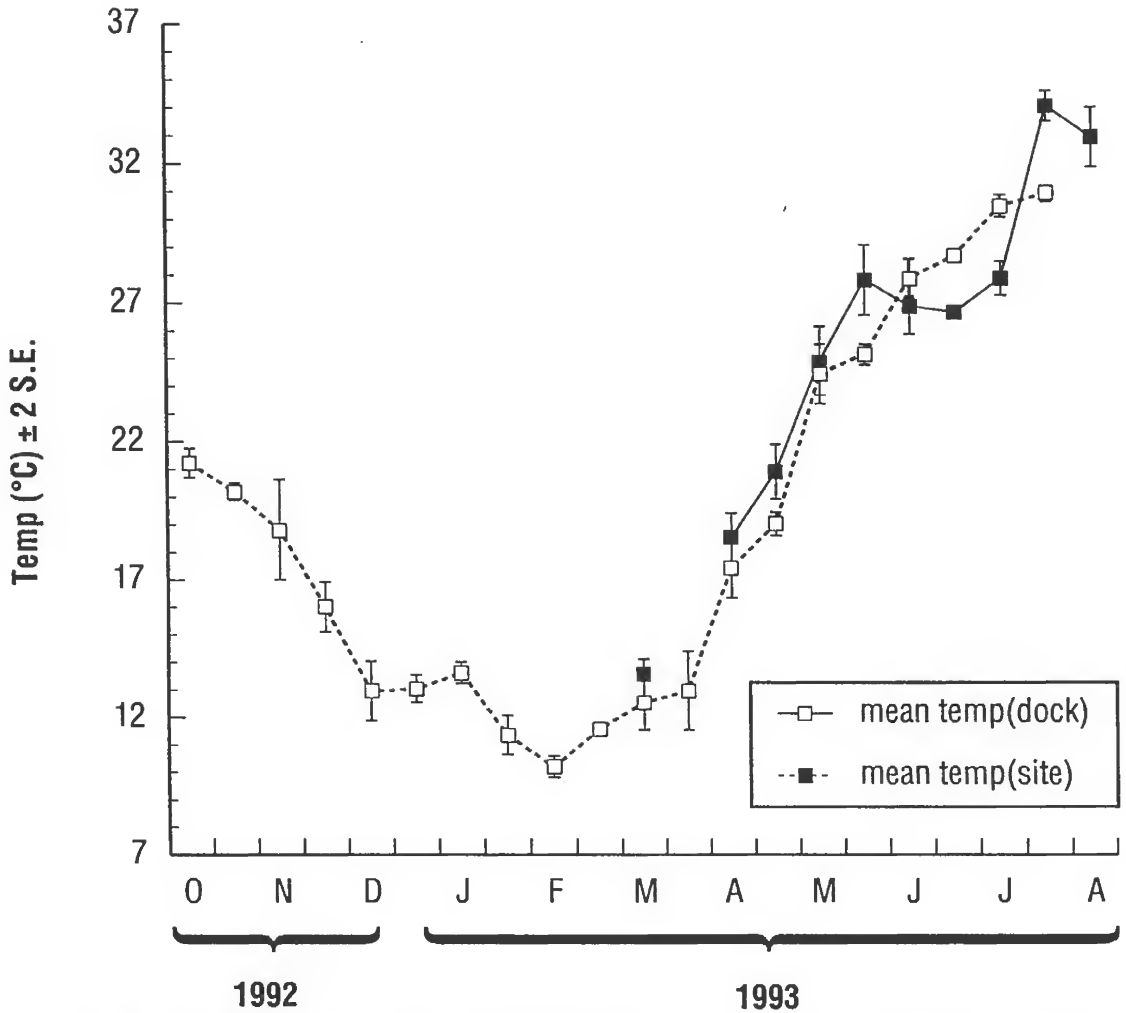
Figure 2. Mean ambient water temperatures taken at the Marine Extension Service Dock, Skidaway River from October 1992 to June 1993 and from the field grow out site from April to August 1993.

were placed on site from March to June 1993. As shown in Figure 2, water temperatures at the dock location are generally representative of temperatures at the test site.

<center>RESULTS</center>

Surf clams grew from a mean shell length of 19.4 mm to 42.6 mm under field conditions from October 1992 to June 1993. Size increased steadily from November until March, remained the same between March ($\bar{x} = 36.2$ mm) and April ($\bar{x} = 35.9$) and increased again from April to June (Figure 3). The decrease in growth rate between March and April was probably caused by the stress endured by the animals when cages were moved to the spring low water mark from the mean low water mark.

Surf clams were inactive (96.6% of total) and early active (3.4% of total) in October 1992 (Figure 4), at a mean water temperature of 21.3°C (Figure 3). By December ($\bar{x}$ temperature = 13.0°C), 83% of the animals ($\bar{x}$ shell length = 25 mm) were in the early active stage. By March ($\bar{x}$ temperature = 12.5°C), 70% of the total surf clams
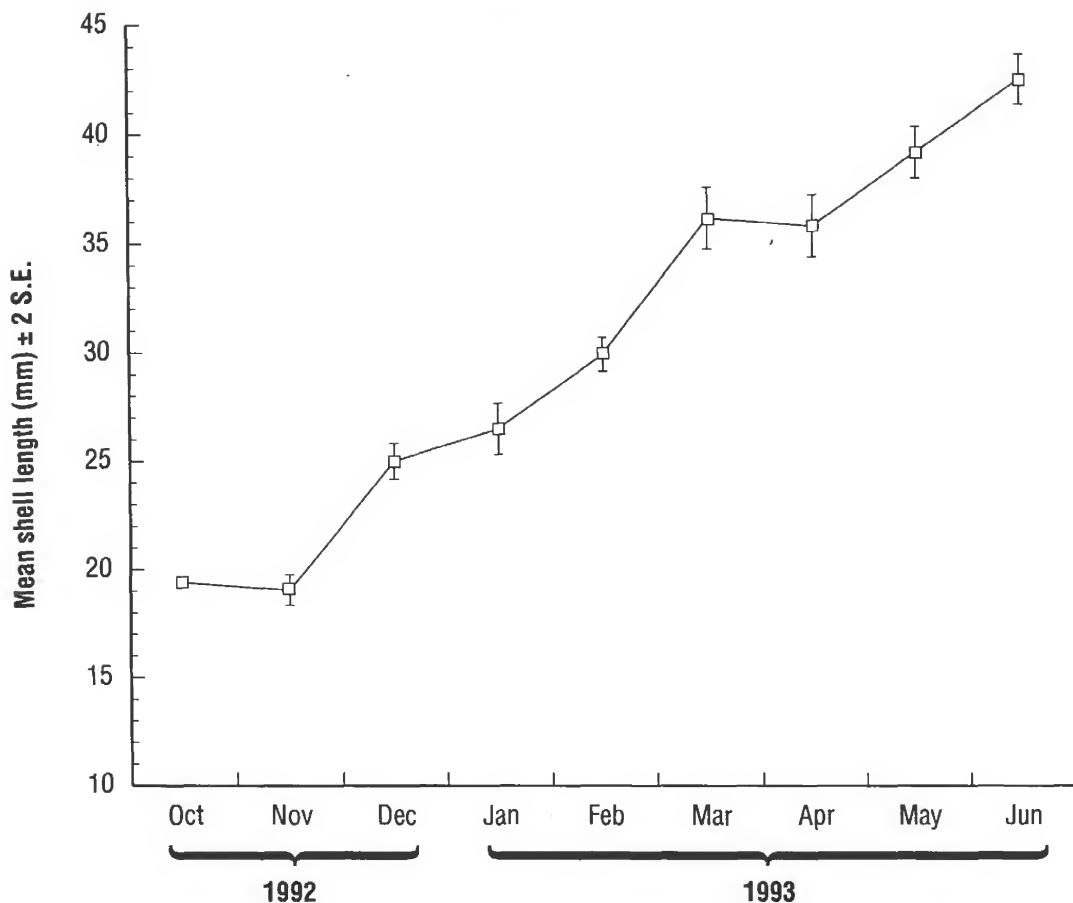
Figure 3. The increase in shell length of the non-native surf clams, *Spisula solidissima*, planted at the mean low water mark on an intertidal sandflat at the mouth of House Creek, Little Tybee Island, Georgia.

collected were in the late active stage. In early April ($\bar{x}$ temperature = 18.5°C), 55.6% of the total surf clams collected were in the late active stage and 44.4% were in the ripe stage. Water temperatures increased steadily and in early May reached a mean of 24.9°C when 17.2% of the surf clams were partially spent, 48.3% were late active, and 34.5% were ripe. By June ($\bar{x}$ temperature = 28.3°C, $\bar{x}$ shell length = 42.6 mm), 39.3% of the clams were spent and 60.7% were partially spent.

Mean gonadal indices for male and female clams are presented in Figure 5. Statistical analysis showed that there were no significant differences (p = 0.8) between male and female gonadal indices; therefore, mean values presented below are combined means of both sexes. Gonadal indices increased to late active stages by March ($\bar{x}$ G.I. = 4.0), with ripe individuals being encountered in April ($\bar{x}$ G.I. = 4.5). Spawning began in May ($\bar{x}$ G.I. = 4.0) and continued into June ($\bar{x}$ G.I. = 1.6) (Figure 4).

A total of 259 clams were histologically sectioned, of which 32.8% were undifferentiated, 45.6% were males, and 32.8% were females. The sex ratio was 0.48 female:1.00 male and significantly differed from parity (χ^2 = 22.09; P < 0.0001).

DISCUSSION

Results of this study indicate that non-native Atlantic surf clams, reared within the coastal waters of Georgia, attained sexual maturity and spawned. In Georgia, spawning occurs in spring at approximately the time that field planted animals must be harvested. Once ambient water temperatures exceed 28°C, total mortality results. Spawning commenced in May after a 7°C increase in temperature from early April ($\bar{x}$ = 18.6°C) through May ($\bar{x}$ = 24.9°C). This pattern reflected that of a population off the shore of
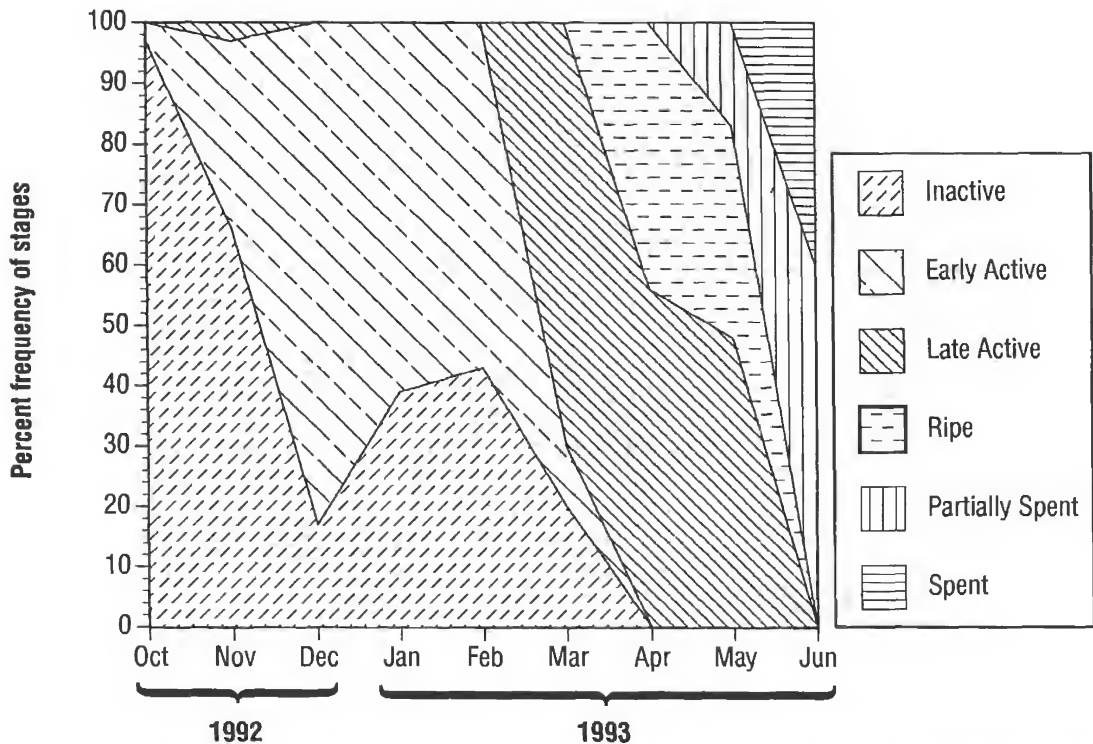
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Figure 4. The percent frequency of surf clams, *Spisula solidissima,* **in each developmental stage for animals cultured in cages at House Creek, Little Tybee Island, Georgia.**

New Jersey as characterized by Ropes (1968). A clam farmer in Georgia could obtain broodstock from field growout plots prior to temperature-induced mortality and the final harvest of the crop. Broodstock could be supplied to a hatchery for either further conditioning in temperature-regulated tanks or animals could be spawned directly after collection. A hatchery operator could produce seed needed for the following fall field planting from yearling animals.

One consideration in using yearling surf clams for broodstock is the unequal sex ratio, since there are fewer females produced within the yearling age group. Unequal sex ratio is not an uncommon phenomenon among juvenile bivalves. In this study, yearling surf clams had a sex ratio of 0.48 female to 1.00 male. Equal sex ratios for surf clams in field populations have been reported (Ropes 1968; Jones 1981; Sephton 1987; Kanti et al. 1993). However, it is not unusual for protandrous bivalves to mature primarily as males within the first breeding season before equal sex ratios occur in older age classes (Joosse and Geraert 1983; Eversole 1989). This has been observed for *Mercenaria mercenaria* (Eversole et al. 1980; Dalton and Menzel 1983; Walker and Heffernan 1995), *Arctica islandica* (Rowell et al.

1990), and *Panope abrupta* (Goodwin 1976; Sloan and Robinson 1984) populations.

Since bivalve fecundity is related to size (Eversole 1989), older, larger females will produce more eggs per spawn. Thus, it would be prudent for the hatchery operator to keep yearling females within the hatchery under regulated water temperatures over summer and replant them in field plots the following fall.

In this study, the Atlantic surf clam achieved sexual maturity within approximately one year when cultured within the coastal waters of Georgia. Spawning occurred between May and June when animals were at a mean size of 39.2 mm and 42.6 mm, respectively. Although the clams were reared in non-native conditions, sexual maturity occurred at a smaller size than previously recorded for *Spisula*. Belding (1910) in Massachusetts found that sexual maturity could occur in yearling surf clams at a size of 39 mm, but that the majority of clams matured at two years of age and at a size of 67 mm in shell length. Ropes et al. (1969) observed that for an inshore population of clams in Chincoteaque Inlet, Virginia, yearling surf clams attained sexual maturity at a shell length of 45 mm. For a
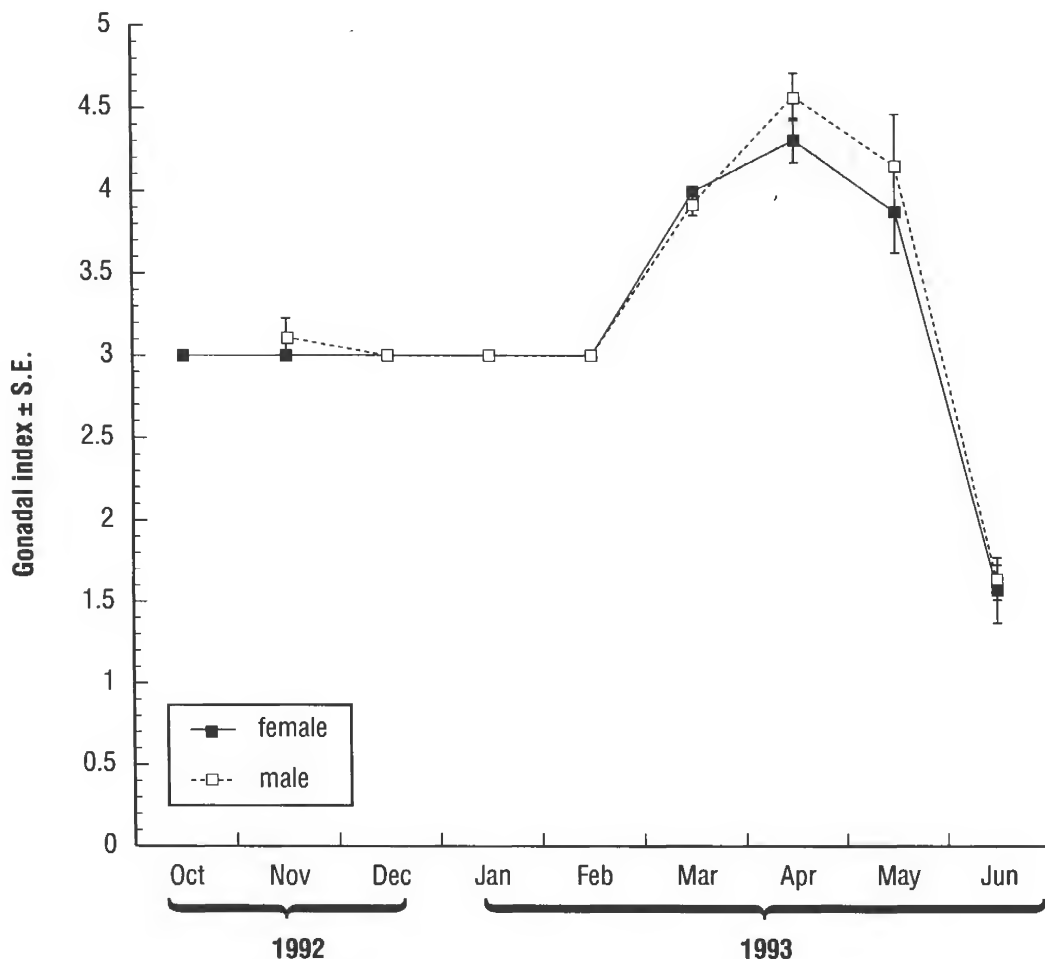
Figure 5. Mean gonadal indices for male and female surf clams, *Spisula solidissima*, cultured in cages at House Creek, Little Tybee Island, Georgia.

Canadian population, sexual maturity occurred at four years of age and at a size of 80 mm (Sephton and Bryan 1990).

In this study, Georgia hatchery-produced seed (19 mm) obtained a mean size of 42.6 mm by June when field planted in Georgia, whereas, in previous studies, a mean size of 60 mm in shell length had been achieved (Walker and Heffernan 1990a,b). The slower growth observed between March and April is probably related to the initial mean low water planting height and disruption caused by cage movement. Surf clams achieve greater size when planted at the spring low water mark and subtidal areas than at the mean low water mark (Walker and Heffernan 1990b).

Thus, greater-sized individuals with a greater potential fecundity can be produced by planting the crop lower in the intertidal zone or in subtidal areas.

If a surf clam aquacultural industry develops in Georgia or the southeastern US, the need for the continual introduction of non-native seed from northern US areas or hatcheries would be eliminated. An aquacultural enterprise in Georgia could obtain broodstock for the production of the following fall's seed crop from the prior year's growout field planted clams before their spring harvest. Thus, once animals are brought into the state under the ICES guidelines for the introduction of exotic species, an industry can be developed from stocks supplied by that single introduction.

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A Note on Bycatch Associated with Deepwater Trapping of Chaceon in the Northcentral Gulf of Mexico

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A NOTE ON BYCATCH ASSOCIATED WITH DEEPWATER TRAPPING OF *CHACEON* IN THE NORTHCENTRAL GULF OF MEXICO

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ABSTRACT Bycatch associated with deepwater trapping of *Chaceon* is reported for outer shelf and slope waters of the northcentral Gulf of Mexico. Bycatch was dominated by the isopod, *Bathynomus giganteus*. Other crustacean megafauna consisted of the majid crab, *Rochinia crassa*, and the portunid crabs, *Benthochascon schmitti* and *Bathynectes longispina*. Finfish bycatch included hagfish, *Eptatretus springeri*, deepwater shark, *Centrophorus uyato* and hake, *Urophycis cirrata*.

MATERIALS AND METHODS

Cruises to establish geographic and bathymetric distribution of *Chaceon* were made in May and August, 1989. Sampling design and protocol are detailed in Waller et al. (this volume). Five areas were sampled; one was located east of the Mississippi River and four were west of the River extending to the Louisiana/Texas border (Table 1).

RESULTS AND DISCUSSION

Four crustacean and five finfish species were collected in association with *Chaceon* trap sets. Occurrence of bycatch by area and depth is listed in Table 2. Distribution of bycatch species is discussed in relation to published accounts of occurrence in the Gulf of Mexico (Gulf of Mexico) and from cruise records of the R/V *Oregon* and R/V *Silver Bay* (Springer and Bullis 1956; Bullis and Thompson 1965).

Crustacean Bycatch

Bycatch was dominated by the isopod, *Bathynomus giganteus*. Highest catches were made in Areas 8 and 9, west of the Mississippi River. Isopods occurred over all depths sampled, but were generally more abundant at depths of 677 and 860 m. They were collected in temperatures ranging from 5.2 to 12.0°C. Bullis and Thompson (1965) found this species widely distributed on mud substrates in the northcentral and eastern Gulf of Mexico at depths from 384 and 549 m over a temperature range of 9.2 to 10.8°C.

Brachyuran crabs trapped in conjunction with *Chaceon* were outer continental shelf/upper slope species whose distribution has been well delineated in the Gulf of Mexico. Their occurrence, as observed in the present study, is consistent with reported data on their geographic and bathymetric ranges. The majid crab, *Rochinia crassa*, was taken in samples east and west of the Mississippi River. Highest catch occurred at 311 m in Area 8. Pequegnat (1970) found this crab at depths from 384 to 732 m and noted that this crab was distributed in all quadrants of the Gulf of Mexico with the exception of the southwest quadrant. Springer and Bullis (1956) reported this species from the northern Gulf of Mexico at stations between 87°25' N latitude and 91°11' W longitude at depths from 357 to 622 m. Crabs in their survey were taken over mud bottoms at temperatures between 10.0 and 10.6°C. Soto (1985) listed *R. crassa* as a characteristic slope species whose distribution was generally limited by the 10°C isotherm. Specimens in the present study were taken at temperatures between 8.4 and 12.7°C.

The portunid crabs, *Bathynectes longispina* and *Benthochascon schmitti*, occurred infrequently and in small numbers. Both species were taken only at 311 m. *Benthochascon schmitti* is widely distributed in the Gulf of Mexico. Pequegnat (1970) listed *B. schmitti* as indigenous to the Gulf of Mexico and noted that it occurred within a narrow range of depth, 201 to 511 m. Springer and Bullis (1956) reported depth distribution from 38 to 472 m; however, the reported occurrence at 38 m is questionable. Soto (1985) grouped this crab with slope species usually distributed below the 10°C isotherm. Bottom temperatures associated with the capture of *B. schmitti* in the northern Gulf of Mexico range from 8.6 to 12.2°C (Springer and Bullis 1956, present study). Powers (1977) reported this species predominant on mud substrates, and Soto (1985) noted occurrence over mud/shell rubble bottoms.

TABLE 1

Station locations by area, depth, latitude and longitude.

Area	Depth (m)	Latitude (°N)	Longitude (°W)
1	494	88° 23.00	29° 03.73
1	677	88° 24.64	29° 00.59
1	860	88° 19.27	28° 59.67
1	1043	88° 19.23	28° 56.02
1	1830	88° 08.59	28° 44.08
6	311	90° 00.01	28° 06.50
6	494	89° 56.83	27° 58.50
6	677	89° 55.88	27° 56.25
6	860	89° 54.74	27° 53.86
6	1043	89° 51.39	27° 47.95
7	311	91° 22.71	27° 50.59
7	494	91° 18.38	27° 47.82
7	677	91° 21.18	27° 44.71
7	860	91° 23.84	27° 43.20
7	1043	91° 25.80	27° 36.56
8	311	92° 04.52	27° 47.78
8	494	92° 11.89	27° 39.98
8	677	92° 12.39	27° 37.65
8	860	92° 13.99	27° 35.44
8	1043	92° 08.77	27° 33.39
9	311	93° 02.21	27° 39.15
9	494	93° 07.77	27° 33.29
9	677	93° 03.00	27° 32.88
9	860	93° 00.11	27° 29.16
9	1043	93° 08.12	27° 22.58

Bathynectes longispina occurred in samples west of the Mississippi River in Areas 7 and 9 in water temperatures of 12.7 and 11.4°C, respectively. Springer and Bullis (1956) found *B. longispina* (listed as *B. superba*) in the eastern Gulf of Mexico from 201 to 476 m at temperatures ranging from 8.9 and 13.9°C. Soto (1985) reported catches from 174 to 403 m in the Florida Straits. This species has been associated with a variety of bottom types, including mud/shell, sand/coral, clay/mud and mud/shell rubble (Springer and Bullis 1956; Soto 1985).

Finfish were collected in small numbers at all areas sampled (Table 2). The hagfish, *Eptatretus springeri*, was the most numerous species taken. Hagfish were captured in all areas with the exception of Area 9. Eighty-eight specimens were collected over depths from 311 to 1043 m. Temperatures

at the time of collection ranged from 5.3 to 12.0 °C. Highest catches were made at 860 m in Areas 1 and 7 in August, with 15 and 18 specimens collected, respectively. Neither Springer and Bullis (1956) nor Bullis and Thompson (1965) reported this species from the western Gulf of Mexico. However, records of occurrence in the western Gulf of Mexico exist, with 10 specimens deposited in the Texas Cooperative Wildlife Collection (TCWC), Texas A&M University (John McEachran, personal communication). Specimens deposited in the TCWC were taken at depths ranging 457 to 781 m. Our data extend both the upper and lower depth limits for this species in the Gulf of Mexico.

Other species taken included the shark, *Centrophorus uyato*; the Gulf hake, *Urophycis cirrata*; muraenid eels; and an ogcocephalid. Springer and Bullis (1956) reported both

TABLE 2

Bycatch associated with *Chaceon* trapping in the northcentral Gulf of Mexico.

Area	Depth	Bathynectes longispina	Benthochascon schmitti	Rochinia crassa	Bathynomus giganteus	Eptatretus springeri	Centrophorus uyato	Muraenidae	Urophycis cirrata	Ogocephalidae
1	494			6	33	4			1	
	677				3	1				
	860 May				4					
	860 Aug				3	15				
	1043					3				
	1830									
6	311*									
	494				78	7				
	677				36	7			1	
	860 May				68					
	860 Aug*									
	1043				2	7				
7	311	2		2				6	2	
	494				5	2				
	677				76	5				
	860 May				64		1			
	860 Aug				32	18				
	1043				39	4				
8	311			43	16	6	1		1	
	494				60					
	677				48	4				
	860 May				131	2				
	860 Aug				42	2				1
	1043				45	1				
9	311	1	2	12						
	494			3	22				2	
	677				109				1	
	860 May				49					
	860 Aug				42					
	1043				57					

* Line Lost

C. uyato and *U. cirrata* (listed as *Phycis cirratus*) from the Gulf of Mexico. The two specimens of *C. uyato* collected in this study were taken in the western Gulf of Mexico at depths of 311 and 860 m, respectively. Gulf hake, *U. cirrata*, were collected in each area in depths ranging from 311 m to 677 m. Springer and Bullis (1956) found this species in the western Gulf of Mexico at depths ranging from 99 to 192 m with the deepest depth recorded at 402 m in the eastern Gulf of Mexico.

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A Pugheaded Cobia (*Rachycentron canadum*) from the Northcentral Gulf of Mexico

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A PUGHEADED COBIA (*RACHYCENTRON CANADUM*) FROM THE NORTHCENTRAL GULF OF MEXICO

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ABSTRACT A pugheaded cobia (*Rachycentron canadum*) captured in the northcentral Gulf of Mexico represents the first record of pugheadedness in cobia. The specimen, a 4-year-old gravid female, exhibited considerable distortion of the premaxillary and maxillary bones, with the length of the snout 46% shorter than that of a normal cobia of the same length. The anomaly had no apparent effect on feeding, since the stomach contained a substantial amount of food, and the fish was the same length expected of a normal 4-year-old cobia.

INTRODUCTION

Pugheadedness has been well documented in many species of marine and fresh water fishes (Dawson 1964, 1966, 1971; Dawson and Heal 1976; Burgess and Schwartz 1975). Genetic abnormalities, embryonic development disorders and aberrations induced by environmental variables are probable causes of this type of anatomical anomaly (Gudger 1928, 1930; Mansueti 1960; Schwartz 1965; Rose and Harris 1968; Hickey 1972; Sindermann 1977; Shariff et al. 1986). Mechanical injury is generally discounted as a primary factor. Pugheadedness has not been previously reported in cobia (*Rachycentron canadum*).

MATERIALS AND METHODS

A pugheaded *R. canadum* was captured on 4 May 1991 by hook and line in the northcentral Gulf of Mexico east of the Chandeleur Islands at 88° 45'N, 30° 00'W in 8 meters of water. Fork length (FL), total weight (TW) and sex were recorded for the specimen. Head measurements of the pugheaded specimen and a normal cobia were taken for purposes of comparison and in accordance with the definitions of Hubbs and Lagler (1964). Stomach contents were removed and examined. The stage of gonad maturation was determined by gross examination. Otoliths (sagittae) were excised from the specimen, cleaned, embedded in Spurr medium and sectioned transversely through the primordium using a Beuhler Isomet low-speed saw. Otolith sections (0.7-mm-thick) were examined under a dissecting microscope using reflected light, and the annuli were counted.

RESULTS

The specimen was an adult female, measuring 1110 mm FL and weighing 15.8 kg TW. The fish had a blunt forehead and an abnormally short upper jaw (Figure 1). A sizable groove extended vertically in the exposed anterior portion of the snout. The exposed tongue and lower oral cavity were partially pigmented. There was considerable distortion of the premaxilla and maxilla, and the snout was tucked downward and slightly inward, affecting the vertical opening of the mouth (Figure 2). The lower jaw was unaltered but did exhibit substantial abrasion around the outer edge of the lip. No exopthalmia was noted. Other aspects of external anatomy appeared to be normal. The head of a normal cobia is shown in Figure 3.

Head measurements of the pugheaded specimen and a non-pugheaded one of the same length and sex (collected by the author) are presented in Table 1. The length of the snout was 46% shorter than that of a normal cobia of the same size. A distance of 44 mm separated the anterior tip of the anomalous snout from the anterior tip of the lower jaw. The frontal bones were slightly elevated resulting in a larger interorbital width and a greater head depth than expected in normal specimens. The head shown in Figure 3 is not the head of the fish described in Table 1.

The stomach contained a 89 mm (total length) croaker (*Micropogonias undulatus*) and a large amount of well-digested fish remains.

Otolith analysis revealed a recently completed fourth annulus. The anomalous specimen's length was comparable with the mean length (1139 mm FL) reported for normal female cobia with otoliths showing a recently completed fourth annulus (Franks and McBee 1992). The back-

calculated FL at annuli I (402 mm), II (768 mm) and III (955 mm) was also comparable with mean back-calculated FL reported for female cobia at ages I (493 mm), II (797 mm) and III (991 mm) (Franks and McBee 1992).

The specimen was gravid with normally developed ovaries.

DISCUSSION

The effects of pugheadedness on the individual depend upon the severity of the anomaly (Hickey 1972). Bortone (1972) postulated that such a condition would typically lead to a lack of competitive ability, but that a moderately pugheaded fish could possibly compete on at least an equal level in regard to feeding mechanism. In spite of the deformity, the anomalous specimen's feeding efficiency apparently had not been significantly limited. The fish was quite robust.

The specimen's length at capture and estimated length at earlier ages indicated that the aberration had not altered growth relative to normal cobia, ages I-IV.

Peak spawning for cobia in the northern Gulf of Mexico occurs during April - May (Lotz et al. 1992). The specimen's ovaries were comparable in appearance to gonads from reproductively active female cobia of similar size collected during May.

The head of the specimen is in the Gulf Coast Research Laboratory Museum, Catalog Number GCRL 26632.

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Figure 1. Frontal view of the pugheaded cobia (*R. canadum*).

Figure 2. Head of the pugheaded cobia (*R. canadum*).

Figure 3. Head of a non-pugheaded cobia (*R. canadum*).

TABLE 1

Comparison of measurements of the head of the pugheaded cobia with the head of a non-pugheaded cobia (each fish 1110 mm FL[1]).

Measurements	Percentage of FL[1]	
	Pugheaded	Non-Pugheaded
Head length[2]	23.8	24.1
Head width	19.8	16.4
Depth of head	20.8	15.9
Least bony interorbital width	13.5	12.7
Length of orbit	2.5	2.4
Length of mandible	9.7	10.2
Snout length	3.6	7.8

[1]Fork length (FL) measured from anterior tip of lower jaw to fork of caudal fin.
[2]Measured from anterior tip of lower jaw to the most distant point of the opercular membrane.

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